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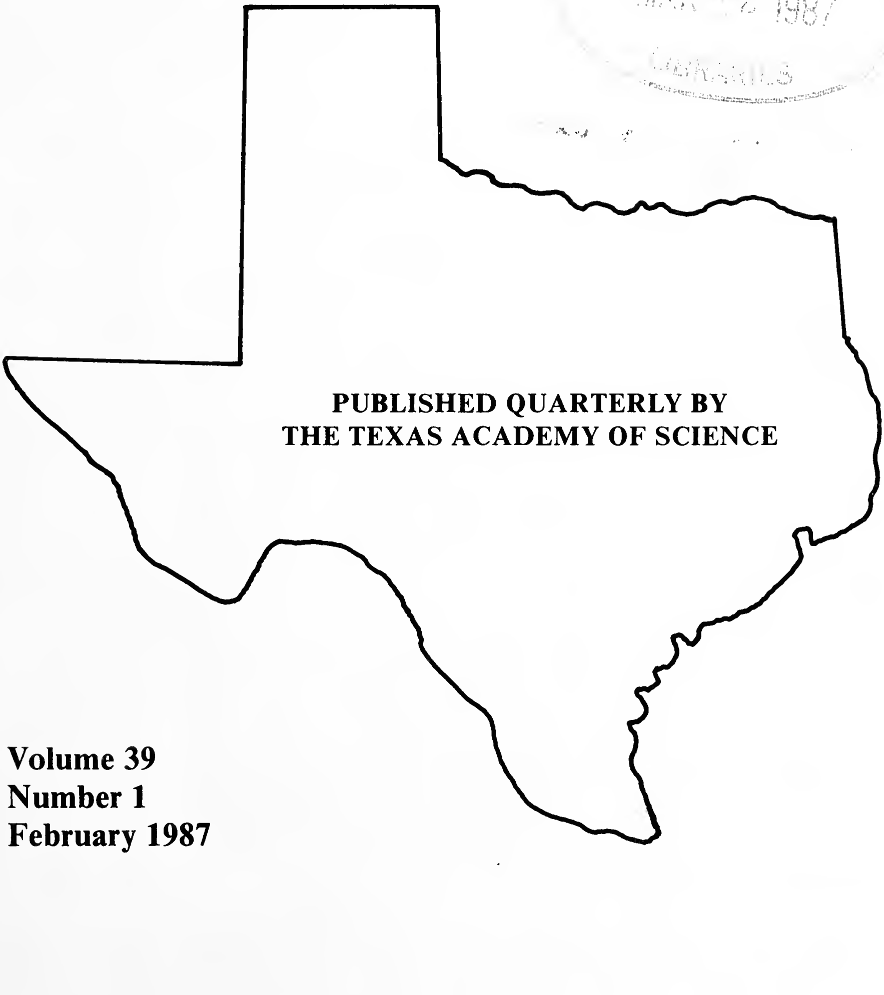

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REPRODUCTIVE AND LIPID PATTERNS OF A SEMIARID-ADAPTED ANURAN, *BUFO COGNATUS*

David R. Long
Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409

Abstract.—Patterns of lipid storage and reproduction of *Bufo cognatus* on the Llano Estacado of northwestern Texas were examined over three years. Seasonal variation in fatbody mass occurred only in females and resulted from changes in the lipid content of the ovaries during dormancy. Histological examination of testes showed a temporal spermatogenic pattern, but no seasonal variation was evident in testis mass, volume, or seminiferous tubule diameter. Ovarian mass showed annual variation, but large follicles were present throughout the activity season. These patterns indicate reproductive readiness throughout the activity season. Liver lipid-free dry mass but not liver lipid mass increased by the end of the activity season suggesting a nonlipid component was the primary energy source for metabolism during dormancy. These patterns of reproductive activity and lipid utilization appear to be physiologically advantageous for an amphibian having moisture-dependent activity regimes but inhabiting a relatively warm and semiarid environment. *Key words.* Anura; *Bufo cognatus*; fatbody; lipid; reproduction.

Lipid is an efficient storage form of potential energy and the strategy employed by a species in allocating stored energy is an important consideration to workers attempting to understand the evolution of reproductive tactics in ectothermic vertebrates. Consequently, annual lipid cycles of species have been the focus of numerous studies (see Derickson, 1976, Fitzpatrick, 1976, and Pond, 1978, for reviews). In sexually mature aquatic and mesic anurans, body lipid is typically low during dormancy as a result of metabolic use, and is used during reproductive activity for vitellogenesis and possibly for steroid production. An increase in stored body lipid occurs after breeding in preparation for winter dormancy (Bush, 1963; Mizell, 1965; Brenner, 1969; Byrne and White, 1975; Chieffi et al., 1975; Pierantoni et al., 1983). Reproductive organs also show seasonal variation with periods of recrudescence and quiescence synchronized around the breeding season (Mizell, 1964; Byrne and White, 1975; Pierantoni et al., 1983).

Arid and semiarid environments present osmotic problems for terrestrial amphibians and usually necessitate brief periods of activity that are coincident with high moisture levels. Because the duration of the activity season and the time available for foraging within the season are major determinants of how much lipid can be stored by an individual in a given year, a study of a species that survives in a semiarid habitat might demonstrate patterns of reproduction and lipid use that are modified to accommodate short and sporadic periods of annual activity.

The semiarid environment and unpredictable summer rainfall of the Llano Estacado of northwestern Texas is relatively harsh for terrestrial

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amphibians. There, the Great Plains toad, *Bufo cognatus*, is intermittently active in spring and summer during times at which moisture and temperature conditions are favorable for activity between dry periods. *Bufo cognatus* is common throughout western Texas and its habitat generally encompasses areas devoid of permanent bodies of water. For this reason, *Bufo cognatus* was used to assess the lipid storage/mobilization strategy employed by an amphibian that has moisture-restricted activity periods. Initial data collected in 1983 indicated this species does not demonstrate a pattern of lipid mobilization typical of temporate zone ectothermic vertebrates (Long, 1985). Therefore, data were collected for three years to examine reproductive and lipid patterns of *B. cognatus* and to compare them to the previously described patterns of mesic anurans. The following hypotheses were tested: 1) *Bufo cognatus* will have low lipid stores on emergence from winter dormancy with a net increase in stored lipid prior to entering the next hibernation period, and 2) male and female gonadal states will change through the activity season with gamete development in the spring and gonadal quiescence at the end of breeding activity.

MATERIALS AND METHODS

Bufo cognatus was collected throughout its activity season in 1983, 1984, and 1985 from an unwatered city park and surrounding roads of Lubbock, Texas. Toads were collected at nights, returned to the laboratory, and refrigerated at 7°C. In 1984 and 1985, male toads were pithed within 48 hours of collection and testes were placed in Bouin's fixative. All individuals were frozen for later processing. In this paper, I examine reproductive and lipid patterns in mature individuals only.

Snout-vent length (SVL) was measured for all toads prior to removal of fatbodies, liver, ovaries, and oviducts. The carcass, minus these organs, was oven-dried at 75°C to constant mass. The diameter of 10 of the largest ovarian follicles from each mature female was measured with calipers in 1984 and 1985 to estimate average mature follicle size. Females without developed ovaries or enlarged oviducts were classified as immatures. Ovaries, oviducts, and livers were weighed for wet mass and oven-dried to constant mass. Fatbodies were weighed in two groups per individual—carcass fatbodies (four pairs of subcutaneous fatbodies and a fatbody anterior to the heart) and gonadal fatbodies. Carcasses and ovaries were ground prior to lipid extraction. Mass was measured to the nearest 0.001 gram.

Lipid extraction of carcasses (minus fatbodies), livers, ovaries, and oviducts was made using chloroform:methanol (2:1, volume/volume—Folch et al., 1957) at 70°C in a Soxhlet apparatus for eight hours (livers, oviducts) or 10 hours (carcasses, ovaries). Extraction times were sufficient as indicated by the dry, nongreasy, powdery consistency of the crushed extracted tissue and the solvent was clear when extractions were terminated. Lipid mass of tissue was determined as dry mass minus lipid-free dry mass.

Testes from toads collected in 1984 and 1985 were embedded in paraffin, sectioned at 7 μm, and stained with Delafield's hematoxylin and eosin. Sexual maturity of males from 1984 and 1985 was confirmed by presence of spermatogenic activity. Sexual maturity of males collected in 1983 was based on comparison of SVL of mature toads collected in 1984 and 1985. During the 70 percent ethanol step of dehydration, maximum length and width of testes (minus Bidder's organ) were measured and combined testis mass (including Bidder's organ) was obtained. Mean testis volume was determined using the equation for determining the volume of a column (volume = $\pi r^2 h$, where r = mean testis width/2 and h = mean testis length). Sectioned testes were qualitatively assessed for spermatogenic activity. In addition to mass and volume, quantitative assessment of testis activity included obtaining the mean diameter of 10 seminiferous tubules per individual.

Toads were assigned to one of five groups based on reproductive patterns of individuals in the year they were collected. The five seasonal groups were determined as follows: 1) posthibernation, premating period (May to first breeding night); 2) the first mating night of each year (7 June 1983, 13 June 1984, 22 May 1985); 3) period of mating activity (after first breeding night through mid-July); 4) period when temperature was still favorable for mating but mating was not observed (late July through August); 5) postmating, prehibernation period (September). Toads collected the first mating night (group 2) were considered premating because they were collected early that night (2100 to 2330 hours), no females were ovipositing, and no eggs were found in the water.

Analysis of covariance (ANCOVA) procedures, using SVL as the covariate, were used to test lipid and reproductive data for intergroup variation. Data to be used in ANCOVA were subjected to Hartley's F-max test to test for homogeneity of group variances (Sokal and Rohlf, 1981) and group-covariate interactions were examined. Natural logarithmic transformation of fatbody mass, carcass lipid mass, liver dry mass, liver lipid mass, and liver lipid-free dry mass for each sex was performed to eliminate heteroscedasticity and group-covariate interaction prior to ANCOVA procedures. Liver lipid-free dry mass was used as the covariate when intergroup variation in liver lipid mass was examined.

Following ANCOVA analysis, *a priori* contrast was made between early (groups 1 and 2) and late (groups 4 and 5) collection groups. This contrast was based on the assumption that if seasonal variation occurred, it would be most evident between early and late samples; thus verifying the variation that was anticipated to occur over dormancy. Linear regression analyses were used to test for relationships between continuous variables. The Statistical Analysis System (SAS) package (SAS Institute, Inc., 1982) was used for all statistical procedures. Statistical significance was determined at $P \leq 0.05$. Means are presented plus or minus two standard errors.

RESULTS

Bufo cognatus initiated activity in May. Few toads were observed on any given night prior to the breeding season. In late May and early June, warm temperatures combined with rain or high humidity stimulated males to aggregate and chorus at local ponds and ephemeral playas. Females were not as numerous as males at breeding sites. By mid-July, breeding activity terminated and toads were again scarce. Mature individuals were no longer observed after late September. Mature males averaged 81.0 mm SVL (n, 91; SD, 11.3 mm; range, 52.0-108.0). Mean female SVL was 94.1 mm (n, 51; SD, 9.6 mm; range, 78.0-112.0).

Males

There was no variation (ANCOVA with covariate SVL) in log transformed fatbody mass (FBM) ($F_{4,84} = 0.31$, $P = 0.87$) or log carcass lipid mass (CLM) ($F_{4,84} = 1.02$, $P = 0.40$) among the five groups (Fig. 1). This lack of seasonal variation in fatbody mass is unusual for anurans. ANCOVA for log transformed liver values indicated intergroup variation for all analyses (Table 1). Contrasts between early and late samples indicated liver lipid-free dry mass (LFDM) was larger at the end of the

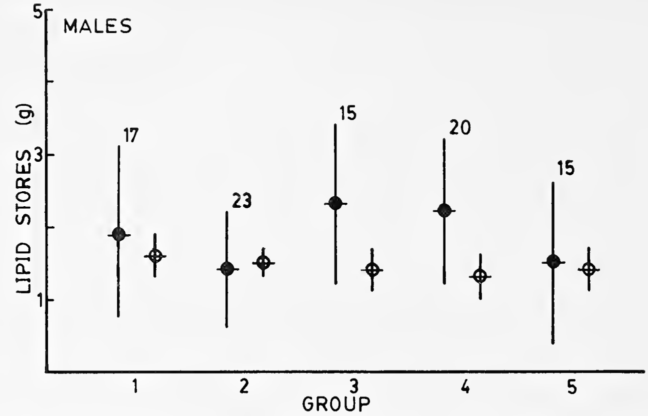

FIGURE 1. Seasonal pattern of SVL adjusted lipid stores in male *Bufo cognatus*. Solid circles = fatbody mass; open circles = carcass lipid mass (minus fatbodies). Mean ± 2 SE. Sample sizes are indicated for each group. See Materials and Methods for group designation.

activity season (F 1,84 = 7.77, $P < 0.01$). Although liver lipid mass, adjusted for liver LFDM, varied significantly among groups, the early-late contrast comparison was nonsignificant (F 1,84 = 0.01, $P = 0.92$) and no biological explanation for the intergroup variation could be discerned.

Mean testis mass, volume, and seminiferous tubule diameter (when adjusted for SVL) remained constant through the activity season (Table 2). Seasonal trends were evident in the spermatogenic process (Fig. 2). Toads collected early in the year (group 1) had large numbers of spermatozoa arranged in bundles or had free spermatozoa in the lumen of the seminiferous tubules (Fig. 2A). Few spermatocytes or spermatids were present in these testes. Toads in groups 2 and 3 showed similar concentrations of bundled and free spermatozoa along with an increased number of primary spermatocytes (Fig. 2B). Fewer spermatozoa were present in group 4 (postreproductive group) (Fig. 2C). In groups 4 (Fig. 2C) and 5 (Fig. 2D), large numbers of germinal cysts containing all spermatogenic stages were present, and most testes exhibited small concentrations of bundled spermatozoa associated with Sertoli cells. The absence of quantitative variation in the testes might have occurred because of the constant replacement of germinal cysts which allowed mature spermatozoa to be available during much of the activity season.

Females

Seasonal variation in log FBM, but not log CLM, was revealed by ANCOVA with covariate SVL (FBM: F 4,45 = 2.55, $P = 0.05$ and CLM: F 4,45 = 1.63, $P = 0.18$) (Fig. 3). A pattern of increased fatbody mass by the end of the season was suggested in Figure 3 and comparisons between early and late groups confirmed a seasonal increase in FBM (F 1,45 = 8.08, $P < 0.01$) but not in CLM (F 1,45 = 0.84, $P = 0.36$).

TABLE 1. Seasonal group values for male *Bufo cognatus* liver parameters.

Group	n	Liver dry mass[1] (g) $\bar{x}$	Liver dry mass[1] (g) 2 SE	Liver lipid mass[2] (g) $\bar{x}$	Liver lipid mass[2] (g) 2 SE	Liver LFDM[1] (g) $\bar{x}$	Liver LFDM[1] (g) 2 SE
1	17	0.450	0.198	0.093	0.064	0.369	0.127
2	23	0.308	0.161	0.141	0.055	0.232	0.103
3	15	0.650	0.205	0.079	0.069	0.511	0.131
4	20	0.613	0.186	0.022	0.063	0.521	0.119
5	15	0.410	0.209	0.121	0.069	0.323	0.133
		ANCOVA					
		F 4,84 = 3.64 $P < 0.01$**		6.63 $P < 0.01$**		5.31 $P < 0.01$**	

Significant differences at $P \leq 0.05$.
ANCOVA based on log transformed values.
[1]Adjusted for snout-vent length.
[2]Adjusted for liver lipid-free dry mass (LFDM).

Log transformed liver values varied among groups (Table 3). Early as compared to late group contrasts indicated an increase in liver LFDM by the end of the activity season (F 1,45 = 8.84, $P < 0.01$). As with males, the early as compared to late group contrast was not significant for liver lipid mass (F 1,45 = 2.15, $P = 0.15$), although intergroup variation was evident with ANCOVA. The highest female liver lipid value was in group 3, possibly representing an increase in vitellogenic activity to replace ova voided during the breeding season. In support of this, the contrast between group 1 and group 3 was significant (F 1,45 = 6.58, $P = 0.01$).

Ovary wet mass and oviduct dry mass varied in the activity season (Fig. 4). As anticipated, ovaries were largest in the beginning of the year and became significantly reduced in size after the start of the breeding season. Ovary mass began to increase by the end of the activity season. Log values

TABLE 2. Seasonal group values for testis parameters of *Bufo cognatus*. All values adjusted for snout-vent length. These parameters were examined for specimens collected in 1984 and 1985, only.

Group	n	Testis mass (g) $\bar{x}$	Testis mass (g) 2 SE	Testis volume (mm^3) $\bar{x}$	Testis volume (mm^3) 2 SE	Tubule diameter (μm) $\bar{x}$	Tubule diameter (μm) 2 SE
1	5	0.072	0.022	80.4	26.0	297.0	43.1
2	6	0.073	0.020	84.6	23.5	249.7	39.0
3	6	0.081	0.023	96.7	26.9	281.4	45.4
4	20	0.064	0.011	83.5	12.8	270.3	22.2
5	3	0.085	0.034	97.4	38.3	258.3	60.8
		ANCOVA					
		F 4,34 = 0.89 $P = 0.48^{NS}$		0.43 $P = 0.78^{NS}$		0.80 $P = 0.53^{NS}$	

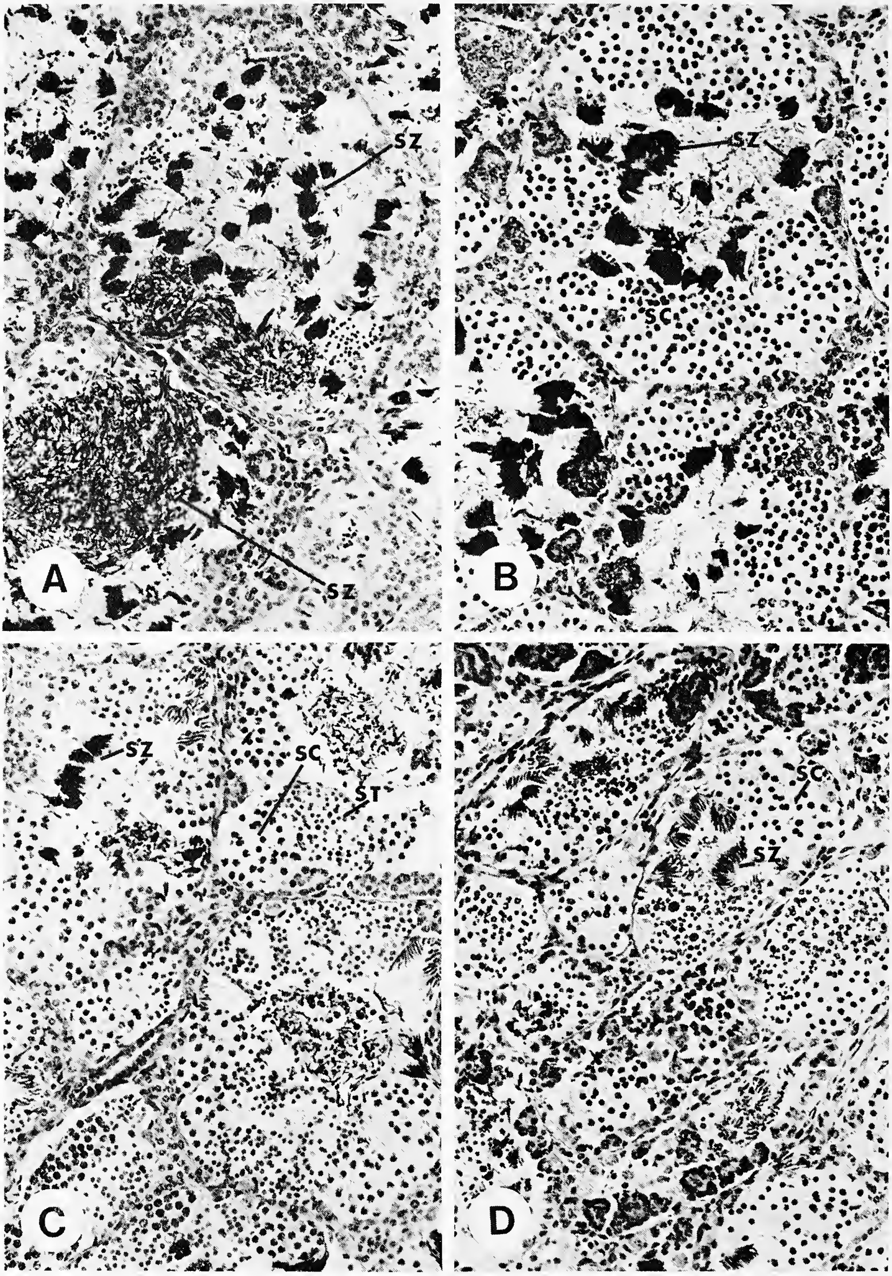

FIGURE 2 (A-D). Temporal spermatogenic pattern of *Bufo cognatus*, × 360. A) Postdormancy individual (group 1) with large concentrations of bundled and free spermatozoa (SZ); B) reproductive individual (groups 2 and 3) with large concentrations of spermatozoa (SZ) and primary spermatocytes (SC); C) postreproductive individual (group 4) with small concentrations of spermatozoa (SZ), but large numbers of primary spermatocytes (SC) and secondary spermatocytes transforming into spermatids (ST); D) predormancy individual (group 5) showing all spermatogenic stages.

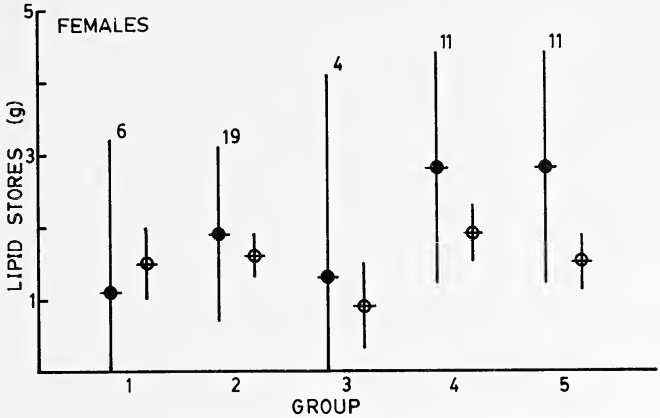

FIGURE 3. Seasonal pattern of SVL adjusted lipid stores in female *Bufo cognatus*. Solid circles = fatbody mass; open circles = carcass lipid mass (minus fatbodies). Mean ± 2 SE. Sample sizes are indicated for each group. See Materials and Methods for group designation.

of FBM and ovary wet mass were not correlated (r = 0.053, n = 49, $P = 0.72$). This was probably a result of follicle retention by females. Oviduct mass followed the same pattern as ovarian mass. Early as compared to late contrasts confirmed the significant reduction in mass of both structures (ovaries—F 1,43 = 26.54, $P < 0.01$; oviducts—F 1,42 = 15.97, $P < 0.01$). Diameter of the largest ovarian follicles did not show intergroup variation (F 4,31 = 1.36, $P = 0.27$), suggesting that mature follicles are available throughout the year. Average large follicle diameter was 1.03 mm ± 0.03 mm (number of females examined, 36).

Ovaries contained 24.3 ± 5.3 percent lipid (n, 24) at their largest mass (groups 1 and 2). Ovary lipid mass increased with ovary LFDM ($r^2 = 0.891$, n = 49, $P < 0.01$). Oviduct lipid mass increased with oviduct LFDM ($r^2 = 0.444$, n = 49, $P < 0.01$). Early as compared to late contrast indicated a larger amount of lipid present in ovaries at the beginning of the season (when adjusted by ovary LFDM) (F 1,42 = 6.31, $P = 0.02$), implying the over-winter increase in ovarian mass also entails a significant increase in the ovary lipid content. The increase in adjusted ovary lipid mass from late to early groups was 0.351 gram.

Variation in female FBM between late and early groups may be explained by lipid used in ovarian enlargement during dormancy. When ovarian lipid mass was added to female lipid stores, seasonal variation in female lipid mass was no longer evident (ANCOVA—F 4,45 = 1.77, $P = 0.15$; early as opposed to late contrast—F 1,45 = 0.15, $P = 0.70$).

Male-Female Lipid Comparisons

Although females possessed larger lipid stores than males (compare Fig. 1, 3), males actually had higher levels of FBM and CLM when SVL was

TABLE 3. Seasonal group values for female *Bufo cognatus* liver parameters.

Group	n	Liver dry mass[1] (g)		Liver lipid mass[2] (g)		Liver LFDM[1] (g)	
		$\bar{x}$	2 SE	$\bar{x}$	2 SE	$\bar{x}$	2 SE
1	6	0.405	0.381	0.102	0.156	0.355	0.287
2	19	0.585	0.210	0.150	0.087	0.464	0.159
3	4	1.117	0.494	0.277	0.191	0.797	0.373
4	11	0.977	0.281	0.107	0.117	0.822	0.212
5	11	0.860	0.282	0.181	0.110	0.663	0.213
		ANCOVA F 4,45 = 3.24 $P = 0.02$*		2.98 $P = 0.03$*		2.78 $P = 0.04$*	

Significant differences at $P \leq 0.05$.
ANCOVA based on log transformed values.
[1] Adjusted for snout-vent length.
[2] Adjusted for liver lipid-free dry mass (LFDM).

used in ANCOVA to adjust for sexual dimorphism in body size (FBM—F 1,139 = 9.97, $P < 0.01$; CLM—F 1,139 = 51.66, $P < 0.01$). SVL adjusted mean values for males were 2.48 ± 0.51 grams (FBM) and 1.81 ± 0.13 grams (CLM), and for females were 1.05 ± 0.68 grams (FBM) and 0.94 ± 0.18 grams (CLM). Lipid sequestered in the ovaries accounted for the lower levels of lipid for females. When FBM and CLM were summed and ovarian lipid mass added for females, no difference in total body fat content was evident between the sexes (F 1,138 = 2.44, $P = 0.12$).

DISCUSSION

The *a priori* hypotheses presented in the introduction were falsified. Only mature female *Bufo cognatus* showed seasonal lipid store variation. Both sexes retained mature gametes throughout much of the activity season and no quanitified testis variation was evident. These patterns appear to be an adaptation to the environmental unpredictabilities present on the Llano Estacado of northwestern Texas. Individual variation in stored lipid, as evidenced by the large standard errors in Figures 1 and 3, is probably a result of variation in amount and types of available food. Dimmitt and Ruibal (1980) calculated that 11 to 12 feedings were necessary to provide metabolic requirements for one year in *B. cognatus* that were dormant 10 months of the year. The tendency to risk foraging during dry weather might vary among individuals and account for much of the within-group variation in the lipid reserve. Examining the reproductive pattern of this species seemed to provide some explanation for the patterns of lipid use.

Males showed no seasonal variation in testis size, so no periodic demand for stored lipid was required for testicular recrudescence. Temporal patterns of spermatogenic activity were evident; however, spermatozoa and

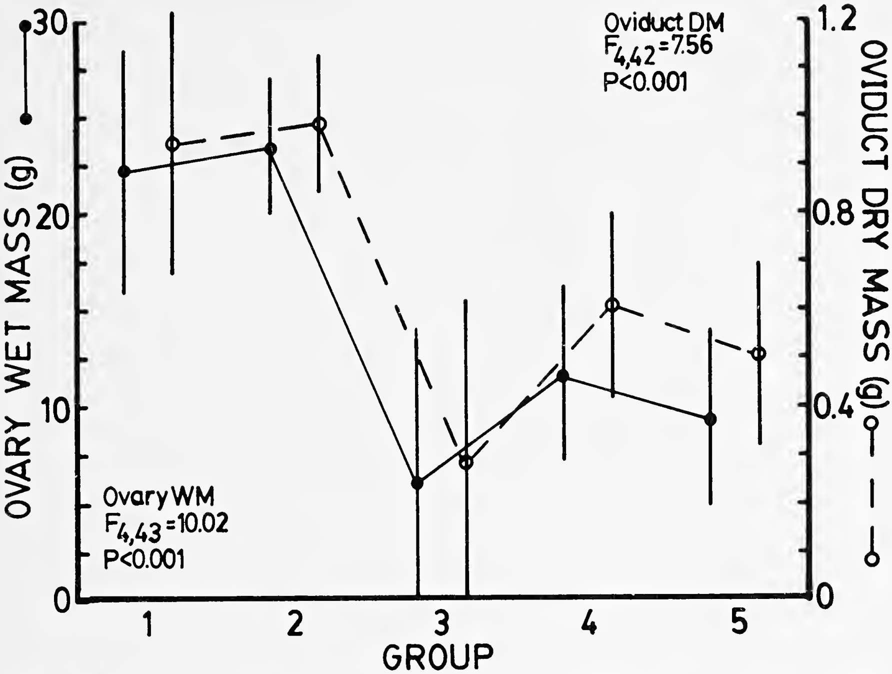

FIGURE 4. Seasonal variation in ovary and oviduct mass of *Bufo cognatus*. Mean ± 2 SE. See Materials and Methods for group designation.

spermatids were present in testes throughout most of the study. Maintaining even low concentrations of viable spermatozoa might be a reproductive adaptation allowing for mating preparedness throughout the activity season, particularly because mating time is contingent on appropriate temperature and moisture conditions (Bragg, 1937, 1940a, 1945). On the Llano Estacado, suitable environmental conditions are not predictable (NOAA, 1983); consequently, males appear to be prepared for mating much of the activity season.

Females presented a similar situation. Ovaries were largest at the start of seasonal activity. During the breeding season, ovary mass dropped to its lowest point; however, females still retained mature follicles of ovulatory size. Ovary mass nearly doubled from this point to the end of the activity season, but was still significantly less than at the beginning. Ovary mass continued to increase during dormancy at the expense of the fatbody stores. Ingestion was probably the primary source of lipid for reproductive processes during the activity season; therefore, the demand on the lipid reserve during that time was minimal. Oviduct mass displayed a seasonal pattern similar to that of the ovaries because of the reduction of secretory products (jelly) associated with ovulation (Jorgensen and Vijayakumar, 1970). Because oviduct lipid mass increased with LFDM, the enlargement of these structures during dormancy also placed a burden on the lipid store.

Van Beurden (1979) described patterns of gamete development similar to those of *B. cognatus* in an Australian desert anuran (*Cyclorana*). As in this study, retention of mature gametes throughout the year appeared to allow for breeding preparedness for times when favorable moisture conditions existed. Bragg (1940b) found ovulatory-size follicles in *B. woodhousei* late in its activity season, leading him to suspect that not all mature females oviposited in a given year. His observation might better be explained by the reproductive pattern demonstrated by *Bufo cognatus*. Females breed, but do not ovulate all mature follicles in a given year, and follicle maturation continues throughout the year. This allows continual breeding preparedness and spreads the demand for protein and lipid for ovarian enlargement over a broader period of time. Therefore, inadequate food ingestion during a dry period might not significantly affect ovarian development.

Energy for metabolism during dormancy in apparently derived primarily from a nonlipid liver material (such as glycogen). Liver LFDM increased by the end of the activity season suggesting a nonlipid component was being stored and then used during dormancy. Liver lipid showed seasonal flux, but no net increase in lipid was evident by the end of the season. Male carcass lipid did not change over dormancy and the variation in females could be accounted for by ovarian lipid requirements.

In conclusion, the amount of fat present in *B. cognatus* probably represents a net accumulation with age and remains seasonally constant when adjusting for individual variation in body size and accounting for ovarian lipid content. Any demands on the lipid reserve for metabolism during dormancy are negligible and a nonlipid material such as glycogen appears to be the main energy source at this time. Females use fatbody lipid for enlarging reproductive structures during dormancy, but most vitellogenic lipid during the active season is apparently obtained from ingestion. By retaining mature gametes throughout the activity season, both sexes are prepared for breeding anytime favorable climatic conditions exist.

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Present address of author: Department of Biology, Wilkes College, Wilkes-Barre, Pennsylvania 18766.

A SURVEY OF THE LEAD DISTRIBUTION IN THE SOIL OF CORPUS CHRISTI, TEXAS

George Harrison
U.S. Geological Survey, Quissett Campus, Woods Hole, Massachusetts 02543

Abstract.—Four-hundred and eighty-five soil samples taken in June 1984 within the city limits of Corpus Christi, Texas, had a mean lead (Pb) value of 208 parts per million with a range of eight to 2969 ppm. A baseline of 13 ppm was established for the community based on remote or virtually untrafficked areas within the city limits. The mean Pb value for samples taken in parks was 55 ppm, for school playgrounds, 57 ppm. All other samples, which were taken from the edges of roadways and freeways, had a mean of 250 ppm. Samples from the northern (oldest) section of the city showed a Pb value 19.5 times above the baseline value, whereas samples from the southern (newer) section of the city showed a Pb value 4.5 times above baseline. The expected correlation of high traffic-flow and increased Pb values was observed except for two instances—lower than expected Pb values around highly trafficked, elevated freeway interchanges, and an inverse relationship between traffic-flow rates and Pb values on a portion of the freeway system. *Key words*: tetraethyl lead; leaded gasoline; vehicular emissions; lead contamination; lead baseline values.

Natural lead (Pb) concentrations can vary from two to 200 parts per million (ppm) depending upon geographical location (Swaine, 1955). Average concentrations of Pb in the soil may range from 10 to 37 ppm (Nriagu, 1978). The mean value for Pb in the earth's crust is 17 ppm and 20 is considered the mean value by some for North America (Nriagu, 1978).

The dominant source of Pb in the urban environment is vehicular exhaust fumes that result from the combustion of gasoline containing tetraethyl lead (Motto et al., 1970; Albasel and Cottenie, 1985). The particulate Pb compounds in exhaust gas cover a wide range of particle size from diameters of 0.01 μm to several milimeters, and reflect vehicle speed. At higher speeds (60 miles per hour), a larger portion of the Pb exhausted is in the form of coarse particles—larger than 5 μm (Hirschler and Gilbert, 1964). Such subtleties help determine the degree of Pb distribution and concentration in an area.

Leaded exhaust emissions produce triethyl lead salts ($Et_3Pb^+X^-$), which are the first degradation products of tetraethyl lead. These salts freely permeate the plasma membranes of mammalian and plant cells, both of which are quite sensitive to the triethyl lead ion (Et_3Pb^+). The high toxicity of this ion, coupled with its ability to pass easily through membranes, makes this compound potentially hazardous to cells of living organisms (Stournaras et al., 1984).

Studies of Pb in soils have shown the increased concentrations in heavily trafficked urban areas of the world (Motto et al., 1970; Ward et al., 1975; Nriagu, 1978; Harrison and Williams, 1982; Lau and Wong,

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1982; Albasel and Cottenie, 1985). Lead variation with soil type, distance from roadways, concentrations in various flora and fauna, and in humans living near roadways also are well documented (Ward et al., 1975; Solomon and Hartford, 1976; Wong and Tam, 1978; Dissanayake et al., 1984; Garcia-Miragaya, 1984). However, detailed overviews of major cities are not available; many works have Pb values based on widely separated sampling sites or in localized segments of a city. Such specialized or localized examinations of Pb concentrations may not give an accurate overview of the actual distribution of Pb or may miss trends characteristic of a given community. Therefore, the intent of this research is to present a detailed overview of Pb distribution in a major city based on numerous closely-spaced sampling sites, and to look for anomalies or trends, or lack of. Such works as this could be of particular interest to urban planners, city traffic divisions, city-county health organizations, environmental scientists, and the general public.

Methods

I sampled 485 locations within the Corpus Christi, Texas, city limits from 19 to 29 June 1984. The numerous parks throughout the city made excellent sampling sites for use as residential Pb indicators and for comparison to roadside soil samples. School playgrounds were sampled where there were no convenient parks. Soil samples were collected from the middle of parks and school playgrounds, grassy medians, grassy roadside embankments and borders, and the grassy areas in and around elevated freeway interchanges. The edge of frontage roads had to be sampled from the Crosstown Expressway (Fig. 1, item J) to Airline (Fig. 1, near item E). These areas provided the only soil samples close to that portion of the freeway (S.P.I.D.—South Padre Island Drive). By sampling only vegetated soil, I felt this helped reduce the possibility of a biased sample from a site where a leaded substance might have been dumped recently. The only consideration given to the soil type was that it not be sandy; more than 99 percent of the samples were clay dominated, whereas two were caliche. This preference for clay soil reflects the dominant soil type for the Corpus Christi area. Sampling the same type of medium also increased the uniformity of samples and sampling technique. The top two centimeters of soil were collected with a Teflon^R knife (a 3.5 by 28 centimeter Teflon^R bar was carved to form a knife). Field samples averaged about 100 grams and were placed in plastic bags. The samples later were ground to a fine powder, homogenized, and subsampled. The average weight of each subsample was 3.5-gram dry weight. These then were placed in Teflon^R beakers, covered with watch-glasses, and refluxed for 24 hours in concentrated HNO_3 under heat lamps. The samples then were dried and the final solution consisted of the sample, 10 milliliters of concentrated HNO_3, and 90 millileters of deionized water. Analyses were performed on a Perkin—Elmer 360 flameless atomic absorption spectrophotometer. A National Bureau of Standards soil sample was used for quality control. Their results were 714 ± 28 ppm of Pb, whereas mine were 694 ± 24 ppm Pb, a difference of three percent.

Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Geological Survey.

Results

The mean Pb value for the city of Corpus Christi, based on all 485 samples, was 208 ppm with a range of eight to 2969 ppm. Samples taken in comparatively remote and untrafficked areas within the city limits yielded a baseline of 13 ppm Pb. In the rural area surrounding the city, a lower baseline is probable. Values that exceeded the proposed baseline of 13 ppm Pb are expressed as a concentration factor (CF) relative to the 13 ppm. Some of the values obtained are listed in Table 1.

The highest concentration of Pb recorded (2969 ppm) was from an embankment of the Crosstown Expressway (Fig. 1, item J) at site 121 (item A). The park with the highest Pb value was Louisiana Parkway with a value of 318 ppm (Fig. 1, item B). It is bounded on either side by a two-lane roadway that is heavily trafficked. The school playground having the highest value (Fig. 1, item C) was Travis Elementary (258 ppm), which is removed from any major streets and is in an older section of the city. Travis is one of the newer schools in the city, having been built in 1980.

A distinct difference existed in the average amount of Pb between the northern (older) and southern (newer) sections of Corpus Christi, with the freeway (S.P.I.D.) being the divider between the two. Exclusive of S.P.I.D. values (62 sites), the area north of S.P.I.D. had a mean Pb value of 254 ppm (CF 19.5). Specifically, northside parks showed a mean value of 66 ppm (CF 5.1), whereas the southside parks had a value of 25 ppm (CF 1.9). North of S.P.I.D., the soils near roadways showed a mean Pb value of 313 ppm (CF 24.1); to the south the value was 67 ppm (CF 5.2).

As expected, the locations with higher traffic-flow rates generally had increased Pb values. Exceptions, however, were the elevated freeway exchanges (Fig. 1, items, F,G,H). They are elevated approximately 10 to 50 feet on a combination of earthen embankments and concrete pillars. Samples taken around the grassy areas of these elevated exchanges were surprisingly low in Pb content (mean of 89 ppm) considering the heavy traffic flow on these structures. Based on traffic-flow rates taken from 14 February through 8 April 1983 by the Texas Department of Public Safety, the vehicular-flow rates for a 24-hour period (v/24 hours) at various locations on Figure 1 were: item D, 97,000 v/24 hours; item F, 61,530 v/24 hours; item G, 29,500 v/24 hours (Subsequent flow rates are from the same source.)

The Crosstown Expressway (Fig. 1, item J) and S.P.I.D. are the two main roadways by which people commute. The Pb distribution was most representative of this (Fig. 1). On S.P.I.D. at item E (Fig. 1), the average traffic flow was approximately 32,500 v/24 hours. The two sampling sites on this section of S.P.I.D. with Pb values greater than 1000 ppm had a mean Pb value of 1172 ppm. Most sites along S.P.I.D. had elevated Pb values. However, the western portion of S.P.I.D, curving northward to intersect I-37, did not, even though the traffice flow was 1.7 times greater (55,340 v/24 hours) than the flow for the eastern portion of S.P.I.D. (from the Crosstown Expressway eastward).

TABLE 1. Lead (Pb) values and ranges for the Corpus Christi, Texas, sampling sites.

Samples	Mean	Range	Standard deviation	Concentration factor (CF) (13 ppm baseline = CF 1.0)
All samples (485 sites)	208 ppm	8-2969 ppm	236	CF 16.2
Parks (94 sites)	55 ppm	8-318 ppm	66	CF 4.2
>1000 ppm (0%)				
100-999 ppm (15%)				
50-99 ppm (17%)				
<50 ppm (68%)				
Schools (12 sites)	57 ppm	11-258 ppm	77	CF 4.4
>1000 ppm (0%)				
100-999 ppm (17%)				
50-99 ppm (8%)				
<50 ppm (75%)				
All others (379 sites)	250 ppm	8-2969 ppm	250	CF 19.4
>1000 ppm (6%)				
100-999 ppm (43%)				
50-99 ppm (15%)				
<50 ppm (36%)				

Ocean Drive, a four-lane, heavily trafficked roadway, follows the northern edge of Corpus Christi. Five of the samples taken along it were in excess of 1000 ppm (Fig. 1; item I, mean of 1291 ppm; item K, 2597 ppm; item L, 1977 ppm). In each case, the sites are located at major intersections. For item I, the traffic-flow was approximately 37,000 v/24 hours and items K and L had an average of approximately 23,000 v/24 hours.

DISCUSSION

Prior studies, as cited in the introduction, have established that Pb exhausted from motor vehicles burning tetraethyl lead is concentrated in and around roadways and is directly proportional to the traffic volume and type of traffic flow. Figure 1 of this study amply reaffirms this. What is of note in this study are: (1) the lower Pb values at the elevated freeway interchanges; (2) the inverse relationship of Pb to traffic flow between the east and west ends of S.P.I.D.; and (3) the differences in Pb values between the older, northern section of the city and the newer, southern section.

A possible explanation for the lower Pb levels around the elevated freeway interchanges may be that particles exhausted at higher speeds are coarser than those exhausted at lower speeds (Hirschler and Gilbert, 1964). Consequently, these larger and presumably heavier coarse-particles would settle out immediately onto the roadway.

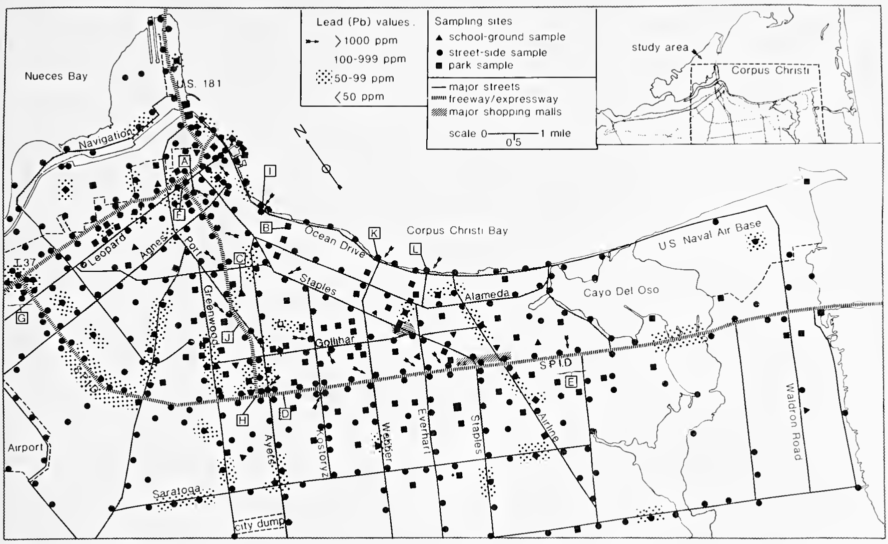

FIGURE 1. Distribution and concentration values of lead within the Corpus Christi, Texas, study area.

The inverse relationship between Pb concentrations and traffic-flow rates at either end of S.P.I.D. probably is attributable to the presence or absence of various traffic lights and closely spaced exit/entry ramps on S.P.I.D. located at major intersections. These slow the flow of traffic considerably at this eastern portion of S.P.I.D. At the west end, traffic moves much more efficiently for there is only one traffic light and few exit/entry ramps. Although the Crosstown Expressway has no traffic lights, it also is burdened with numerous exit/entry ramps that slow vehicular traffic during peak periods of traffic flow. Consequently, there are high Pb levels along its length. Of the 20 sampling sites with Pb values in excess of 1000 ppm, 11 are associated with the Crosstown Expressway and S.P.I.D. (east end) freeway system.

The main concentration of Pb exhausted from traffic generally is limited to a narrow zone within 100 meters of a roadway (Nriagu, 1978). Consequently, the Pb is capable of being concentrated in the older and more congested portions of a city. Kinard et al. (1976) noted that freeway vehicular emissions enveloping certain metropolitan areas, coupled with emissions from inner-city traffic flow, present a potential hazard to the health of inner-city residents. This may apply to vehicular emissions in general because Pb is not the only contaminant exhausted (for example, chlorine, bromine, sulfur, and carbon monoxide).

Of special note are the higher mean Pb concentrations found north of S.P.I.D. as compared to those of the south. While the area north of S.P.I.D. carries the greater traffic burden, it is also the older section of

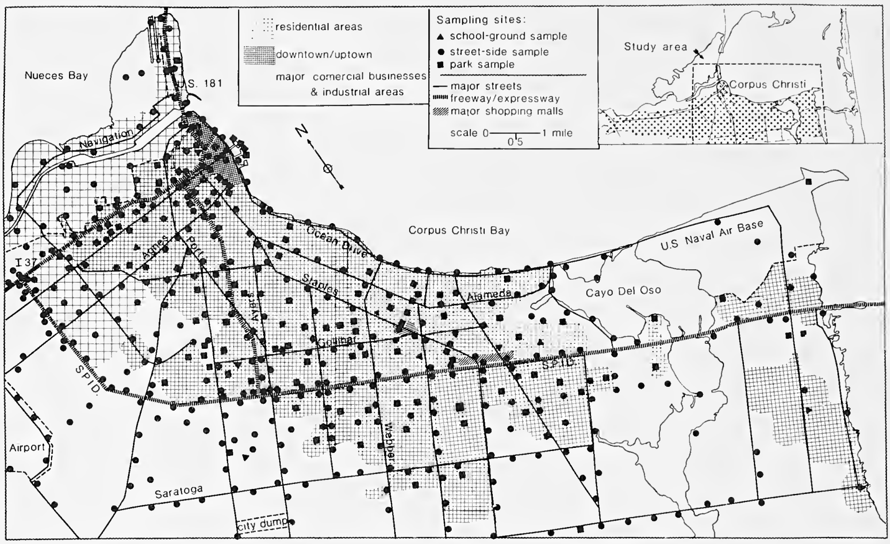

FIGURE 2. Distribution of residential and nonresidential areas within the Corpus Christi, Texas, study area.

town. Therefore, in addition to the concern for general exposure to exhausted Pb, length of exposure time to Pb emissions is an additional health question. The area to the south of S.P.I.D. is comparatively new. Development there did not begin until about 25 years ago and major expansion has occurred within the last 10 years. Until development of the southside, all major residential areas were confined to the north side of S.P.I.D. The major industrial locations have not changed and most commercial businesses blend in with the residential areas in the form of small strip-shopping centers, individual business structures, and major shopping malls. Older and larger commercial businesses (mainly industrial suppliers) are confined to the northwest segment of the city (Fig. 2). As Figure 2 shows, the residential area is extensive and well segregated from the major industrial and commercial enterprises.

The section of the city bisected by the Crosstown Expressway (Fig. 1, item J) contains some of the oldest residential areas in the city. Second- and third-generation families live within this area and many schools are located there. This implies a consistant and long-term exposure of the residents to exhausted Pb. This potential hazard is demonstrated in two related studies dealing with house dust. House dust in inner-city homes of Boston averaged 2000 ppm Pb (Kreuger, 1972), and in Champaign-Urbana, Illinois, Solomon and Hartford (1976) found home-interior dusts averaged 600 ppm and nonresidential interior samples averaged 1400 ppm. "Such contamination for home interiors could pose serious health problems for small children or infants who enjoy placing fingers and toys into their mouths; there will inevitably be some fraction of this contaminated dust on the toys or fingers" (Solomon and Hartford, 1976).

Even though the average Pb content of gasoline has declined, the total discharge in the environment still is considerable if the increase in consumption is accounted for (Rodriguez-Flores and Rodriguez-Castellon, 1982). Even with the mandatory no-lead gasolines beginning in 1986 for the United States, the lead problem probably will be with us for some time. The residence time of Pb in urban dust and soils is unknown and will vary according to the geographic, climatic, and topographic conditions of each city. In coastal communities such as Corpus Christi, much of this Pb is washed into the surrounding bays, estuaries, and seas via storm and street drains. Pb can be concentrated even further in sediments and organisms near the outfalls of these drains (Holmes, 1974; Harrison and Martin, 1982; Harrison, 1984).

Conclusions

The three main factors influencing Pb concentrations from vehicles are: (1) proximity to the source; (2) volume of traffic; and (3) the loitering time of this volume of traffic in a given area as the result of traffic signals, reduced speed limits, and congestion resulting from closely spaced exit/entry ramps. As shown in this study, the impact of these factors may be magnified in the older, more congested sections of a major urban community. How great a factor the local wind conditions are in dispersing or concentrating the Pb was not studied. Although Corpus Christi has a high average wind velocity (12 to 13 miles per hour) and the wind is dominately from the south in the summer months, areas sampled on the far north side of the city did not demonstrate any unusual buildup nor was there a graduation of values across the city coincident with wind direction.

Such studies as this are not statements on the toxicity of Pb, but only on its relative availability and actual distribution. However, high Pb values present a greater potential for toxicological repercussions than do low values. Even though leaded gasolines soon will not be permitted in the United States, as long as there are combustion engines and increasing numbers of people to use them, traffic emissions in general will continue to produce the spector of potential ill-health.

Acknowledgments

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A STUDY OF THE $Cu(H_2O)_6^{2+}/CuCl_4^{2-}$/ETHANOL SYSTEM FOR SOLAR ENERGY STORAGE

L. Gene Spears, Jr., Larry G. Spears, and Joycelyn C. Spears

Department of Chemistry, Rice University, Houston, Texas 77005; Department of Natural Sciences, University of Houston-Downtown, Houston, Texas 77002; and Science Department, Cypress Creek High School, Houston, Texas 77070.

Abstract.—In ethanol, $CuCl_2 \cdot 6H_2O$ can establish an equilibrium between the hydrated Cu(II) ion and the tetrahedral copper chloride anion. This reaction provides a potential means of storing solar energy via the unhydrated $CuCl_4^{2-}$. On cooling, heat is released based on the heat of hydration and the specific heat of the solution. To determine the potential capacity of this system for energy storage, the solubility of cupric chloride in ethanol at different temperatures, the ΔH_{hyd}, and the specific heat of the solution were determined. Theoretical calculations then were made to compare the heat storage capacity of the $CuCl_2 \cdot 6H_2O$/ethanol solutions to that of water, for a solar energy collection system. *Key words*: solar energy storage; hydrated salts; solubility of copper chloride; heat of hydration; heat capacity.

One of the major problems associated with the utilization of solar energy as a primary energy source for heating and cooling is the lack of a practical, efficient means of storing large amounts of energy after it has been collected. Sensible heat storage via heated liquids or rocks has the disadvantages of low energy density and requires large volumes for limited collector temperatures (Wentworth et al., 1981). Latent heat storage, which utilizes the heat associated with phase changes, normally from solid to liquid, also is utilized as a method for solar energy storage (Meinel and Meinel, 1979). Another method for storage utilizes a reversible endothermic reaction (Wentworth et al., 1981).

In a previous study (Spears and Spears, 1984), it was shown that a solution of cobalt (II) chloride in isopropyl alcohol could be used for storing solar energy via the reversible reaction between the hydrated cobalt (II) ion and the chlorinated cobalt (II). In addition to the specific heat of the solution, this system utilizes the heat of hydration for the cobalt (II) ion for additional heat storage capacity. For this system, the value of the equilibrium constant and the solubility as a function of temperature determine the potential for heat storage. Based on the above research, solutions of the hydrated salts of $Al_2(SO_4)_3$, $Cr(NO_3)_2$, $CuCl_2$, Fe $(NO_3)_{,3}$, $FeCl_3$, and $NiCl_2$ in ethanol were selected for preliminary screening. Of these, $CuCl_2$ appeared to be the most desirable and was chosen for further study. In making this choice, several factors were considered: 1) the solubility of the salt; 2) the sensitivity of the system to temperature change and the ability to reach equilibrium quickly; 3) the heat of hydration of the salt; and 4) the availability of a convenient

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instrumental method of analysis to follow changes in the equilibrium system. This last factor prevented the consideration of many hydrated salts. Because water is a part of the equilibrium reaction, its concentration in the solvent is important.

When $CuCl_2{\cdot}(H_2O)_6$ is dissolved in ethanol, the following equilibrium is established:

$$Cu(H_2O)_6^{2+} + 4Cl^- \rightleftharpoons CuCl_4^{2-} + 6H_2O.$$

In this system, the forward reaction is endothermic and the reverse reaction is exothermic. Thus, the forward reaction could be used to collect and store solar energy, whereas the reverse reaction could be used to release the stored energy.

A series of experiments were performed using the $CuCl_2{\cdot}6H_2O_6$ ethanol system to determine its potential use as an energy storage medium. Because $CuCl_4^{2-}$ had a distinct green color and $Cu(H_2O)_6^{2+}$ is blue, visible spectrophotometry was used to follow the reaction. Using the recorded data and published information, calculations were made to compare the heat storage capacity of this system to that of water, for a solar energy collection system.

Experimental Section

The majority of the experimental research was concerned with following the reactions of $CuCl_2{\cdot}6H_2O$ dissolved in ethanol, by the use of a Model-2 Perkin Elmer recording spectrophotometer with a controlled temperature cell attachment, in the visible region of the spectrum. Because the green $CuCl_4^{2-}$ complex has a major absorption peak at 281 nm and the $Cu(H_2O)_6^{2+}$ complex does not absorb in this region, a Beer's Law calibration plot was determined using a cell pathlength of 1.0 centimeter. A value of 288 M^{-1} cm $^{-1}$ for the molar absorptivity constant was calculated from the resulting linear plot.

Because the $CuCl_4^{2-}$ and $Cu(H_2O)_6^{2+}$ions were the only Cu-containing ions detected in the test solutions, the total concentration of dissolved Cu^{2+} was assumed to be equal to the $CuCl_4^{2-}$ concentration plus the $Cu(H_2O)_6^{2+}$ concentration.

The ethyl alcohol used in this study was 99.9 percent pure, with less than 0.005 percent water. The copper (II) chloride used had a purity of 99.5 percent. It was pulverized and heated, at 150°C for three hours, to dryness. All weighings and sample transfers involving the anhydrous copper chloride were done in a dry box.

Results

Determination of Product/Reactant Ratios

Due to difficulty in measuring values for the free water concentration, values for the product/reactant ratio

$$\frac{[CuCl_4^{2-}]}{[Cu(H_2O)_6^{2+}]}$$

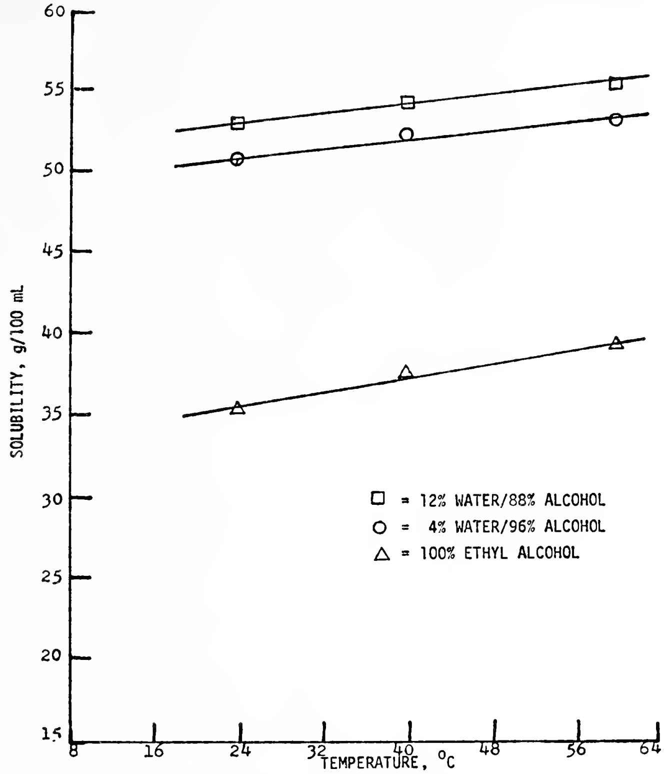

FIGURE 1. Solubility of $CuCl_2 \cdot (H_2O)_6$ in ethyl alcohol/H_2O solutions at different temperatures.

were used instead of K_{eq}. These ratios were determined at various temperatures and water concentrations for 0.002 M $CuCl_2$ solutions (Fig. 1). From these data, the percent $CuCl_4^{2-}$ present in each solution was determined (Table 1).

Solubility of $CuCl_2 \cdot 6H_2O$ in Ethanol

Saturated solutions of $CuCl_2$ with varying water concentrations were heated to three different temperatures and their absorbances at 281 nm were recorded. Concentration values for $CuCl_4^{2-}$ were determined and using the data in Table 1 the corresponding concentration values for $Cu(H_2O)_6^{2+}$ were calculated. These two values were added together to obtain the total solubility as a function of temperature and water concentration (Fig. 2). The solubility value for 24° C and four percent water compares favorably with a reported value of 53g/100mL in 95 percent ethanol at 15° C (Perry and Chilton, 1973).

TABLE 1. Percent composition of 0.002 M $CuCl_2$/ethanol solutions.

%H_2O	T(°C)	% $CuCl_4^{2-}$	% $Cu(H_2O)_6^{2+}$
4	24	48.9	51.1
4	40	58.0	42.0
4	60	66.5	33.5
8	24	23.2	76.8
8	40	41.3	58.7
8	60	53.0	47.0
12	24	2.15	97.8
12	40	27.7	72.3
12	60	43.0	57.0

Determination of Specific Heat

The specific heat of a solution describes the amount of heat it can absorb. A 0.1 M solution of copper (II) chloride in 88 percent ethanol was assumed to be representative for this system and a modified Nalgene Dewar flask/calorimeter was used for the specific heat measurements. Following the procedure described by Morss and Boikes (1978), an average value of 4.20 J g^{-1} °C^{-1} was obtained for the specific heat using 50 mL samples at 24°C and an initial calorimeter temperature of 40°C.

Determination of the Heat of Hydration

In addition to the specific heat, the $CuCl_2$/ethanol solution is capable of storing heat via the $CuCl_4^{2-}$ tetrahedral complex. On cooling, this complex can revert to its hydrated form, $Cu(H_2O)_6^{2+}$, and in doing so releases heat due to hydration (ΔH_{hyd}). By use of conventional methods (Shiflett, 1978), a value for $\Delta H_{hyd} = 63.2$ kJ $mole^{-1}$ was determined. A theoretical value of -66.5 kJ $mole^{-1}$ can be calculated from published thermodynamic data (Perry and Chilton, 1973).

Energy Storage Calculations

The heat storage capacity of a solar heating system using the $CuCl_2$/ethanol system as the energy storage medium was calculated based upon data collected during this study.

The solar collector was assumed to concentrate incoming heat at a 4:1 ratio, and to operate at a mean temperature of 60°C. Using Figure 1, the concentration of copper chloride in a saturated solution of 88 percent ethanol was determined to be 2.27 M at 60°C.

The heat content of solution is due both to the heat of hydration and the specific heat. In Figure 2, it is seen that for 88 percent ethanol at 60°C, the $CuCl_4^{2-}/Cu(H_2O)_6^{2+}$ ratio is 0.768, and at 20°C it decreases to 0.0219. From these values it can be determined that at 60°C, 43.4 percent of the copper is unhydrated, and at 20°C, 2.1 percent is unhydrated. Thus on cooling from 60°C to 20°C, 41.3 percent of the $CuCl_4^{2-}$

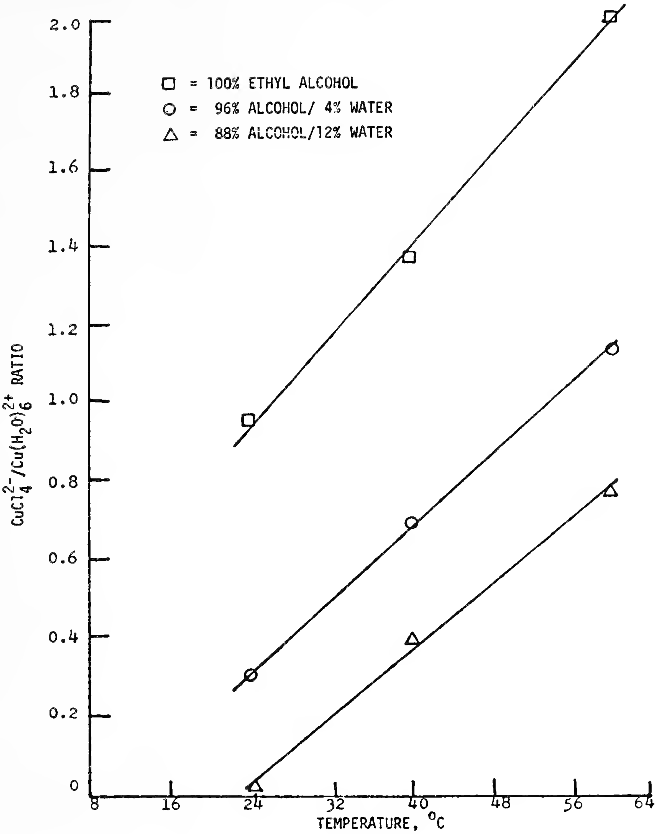

FIGURE 2. Effect of temperature on the $CuCl_4^{2-}/Cu(H_2O)_6^{2+}$ ratio at different H_2O concentrations.

undergoes hydration. The heat released from 1.0 L of 2.27 M $CuCl_2$ in ethanol for this amount of hydration would be

$$63.2 \text{ kJ mole}^{-1} \times 2.27 \text{ mole L}^{-1} \times 0.412 = 59.3 \text{ kJ L}^{-1}.$$

The specific heat of 1.0 L of the above solution is approximately

$$4.20 \text{ J g}^{-1} \, ^\circ\text{C}^{-1} \times 0.80 \text{ mL}^{-1} \times 1000 \text{ mL L}^{-1} = 3.36 \text{ J}^\circ\text{C}^{-1} \text{ L}^{-1},$$

where 0.80 g mL^{-1} equals the assumed density of the solution (this value would vary depending on the concentration of dissolved salt and temperature). If the temperature of the cool solution is 20° C and that of the heated solution is 60° C, the total heat absorbed per liter would be

$$59.3 \text{ kJ}^{-1} + 3.36 \text{ kJ } ^\circ\text{C}^{-1} \text{ L}^{-1} \times (60^\circ\text{C-}20^\circ\text{C}) = 194 \text{ kJ L}^{-1}.$$

This calculation assumes that the value of ΔH_{hyd} remains constant in the temperature interval 20-60° C.

If water was used as the storage medium under the above conditions, it would have a total heat absorption capacity of

$$4.18 \text{ kJ } {}^\circ\text{C}^{-1} \text{ L}^{-1} \times (60^\circ\text{C}-20^\circ\text{C}) = 167 \text{ kJ L}^{-1}.$$

Discussion

In the above, it has been shown that the copper (II) chloride/88 percent ethanol system has a theoretical energy storage capacity approximately 16 percent greater than that of water assuming that $\Delta T=40^\circ C$. Figure 2 indicates that large values of ΔT would favor this type of system. Our data indicate that this equilibrium system adjusts rapidly when the temperature is changed. An additional advantage to this system is the lower freezing point than that of water.

It is not proposed that this system be pursued on a commercial basis due to the obvious high cost for the solute. However there are other hydrated salts that are less expensive, more soluble, and have higher heats of hydration that copper (II) chloride that may be economically and thermodynamically suitable for this purpose. Based on this research, it is recommended that liquid phase equilibra systems involving hydrated salts be considered as a method for storing solar energy in systems where pumping of the liquid storage medium is required.

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RELATIVE MOBILITY OF LEAD AND COPPER IN SOILS: AN EXAMPLE FROM THE BONANZA DISTRICT, SAGUACHE COUNTY, COLORADO

JOSEPH C. CEPEDA

Department of Geosciences, Killgore Research Center, West Texas State University, Canyon, Texas 79016

ABSTRACT.—The relative mobility of Pb and Cu in the soil profile downslope from tailing piles in mining districts is a function of climate, relative solubility of metal sulfates, slope, pH, and soil type.

In the Bonanza District, Saguache Co., Colorado, 50- to 85-year-old mine dumps with more than 4400 parts per million of lead and 970 of copper show a narrow, well-defined dispersion train downslope from the dump. Mobility of copper on this steep (29 degrees) slope is limited relative to that of lead. Copper contents in the soil approach background values (50 ppm) approximately 60 meters down the slope, but lead contents 80 meters down the slope are still four to five times the background value of 500 ppm.

The dispersion haloes are probably produced by downslope movement of resistant metallic sulfides and possibly native copper particles on a steep slope in a semiarid climate.

Key words: soils; Colorado; geochemical prospecting.

The bulk of the exposed economic ore deposits on the earth's surface already have been discovered by conventional geologic and field techniques. Additional reserves of metallic minerals remain hidden beneath a few centimeters to a few meters of soil, alluvium, or glacial debris.

Geochemical prospecting techniques seek to locate these hidden bedrock deposits by identifying their anomalous, metal-rich haloes composed of metallic elements dispersed in the soil horizon in a general downslope or downstream direction from the deposit. An anomalous concentration is generally defined as more than three times the background value for that element. Background values can be determined by regional geochemical surveys such as the National Uranium Resource Evaluation (NURE) surveys or by values obtained from samples sideslope or upslope from mine dumps or ore deposits.

Previously exploited mining districts contain the combination of factors necessary to produce an ore deposit, and in geochemical surveys of such areas it is desirable to be able to confidently distinguish between anomalies produced from an old mine dump and those produced by previously undiscovered mineralization. This type of study also has environmental implications—that is, defining the extent and degree of metallic contamination of soils and surface and subsurface waters.

The Bonanza Mining District was selected for this study because it is mineralized by several elements, including lead and copper. Relative values of Pb and Cu in soils downslope from the dump compared to values from samples taken from the mine dump indicate relative element mobility. The objective of this study was to evaluate and compare the geometry and size of the dispersion haloes for both Cu and Pb.

GEOLOGY AND MINERALOGY OF THE BONANZA DISTRICT

The Bonanza Mining District, Saguache Co., Colorado, is located in the extreme northeastern part of the San Juan volcanic field in south central Colorado. Named for the town of Bonanza on Kerber Creek, it encompasses an area of about 100 square kilometers (30 square miles). The highest peaks in the district have elevations of 3660 meters (12,000 feet) to 4000 meters (13,200 feet). The elevation of the town of Bonanza is approximately 2850 meters (9400 feet) above sea level. Slopes are steep and many in the northern part of the district are heavily wooded with spruce, Douglas fir, Ponderosa pine, and aspen. In the southern part of the district, the vegetation is more sparse, particularly on south-facing slopes.

Precipitation in the district is a function of altitude and occurs as thundershowers in summer and moderate to heavy snowfall in winter. Average annual precipitation at the elevation of the study area is about 45 centimeters (18 inches).

Burbank (1932) described the distribution and structure of the Paleozoic sedimentary units and the Tertiary volcanic sequence and intrusive rocks in a comprehensive investigation of the geology of the district. The main deposits of the Bonanza District are veins containing Pb, Zn, Cu, and Ag. Mineralogically, these veins contain pyrite, sphalerite, galena, chalcopyrite, bornite, and silver-bearing tennantite in a gangue of calcite, quartz, rhodocrosite, and barite (Burbank, 1932).

Burbank (1932) was the first to recognize a collapse feature in the district, which he suspected may have been formed by the eruption of magma from beneath the Bonanza area. Subsequent investigators (Karig, 1965) have recognized the Bonanza Caldera, one of 18 known or inferred calderas in the San Juan volcanic field.

Most of the productive veins cut the Rawley Andesite, a sequence of intermediate composition volcanic rocks older than the 36 million-year-old Bonanza Caldera (Burbank, 1932; Varga and Smith, 1984). Ore-bearing veins also cut the Bonanza tuff of dacite to rhyolite composition (Varga and Smith, 1984). It was the eruption of the Bonanza tuff 36 million years ago that caused the formation of the Bonanza Caldera.

The mining history of the district began in 1879-80, and the majority of the metal output occurred between 1904 and 1930, when the Rawley mill was closed and its equipment sold for salvage value (Burbank, 1932). Thus, the majority of the tailings in the district are 50 to 85 years old.

Yenter (1984) mapped the soil in the study area as a Bushvalley cobbly loam. This is a shallow, well-drained soil with moderate permeability and typical of mountain slopes and ridges. This soil type contains 15 to 35 percent clay and two to three percent organic matter. Soil pH ranges from 6.1 to 7.8. (Yenter, 1984).

Sample Collection and Preparation

Soil samples were collected at depths of 10, 20, and 30 centimeters at 19 points downslope from a mine tailing dump in June 1981. Four samples were collected from various parts of the mine dump itself, as shown in Figures 1 and 2.

Individual samples were taken at each depth along three traverses spaced 36 meters (120 feet) apart. Sample spacing along the traverse lines was nine meters (30 feet). See Figures 1 and 2. Bedrock outcrops in the vicinity of the dump area consisted of andesitic volcanic breccias of the Rawley Andesite. The grassy slope downhill from the dump has a slope of 29 degrees to the southeast.

The 30 to 60 mesh and less than 60 mesh fractions were processed, digested in a hot acid bath, and analyzed for Pb and Cu by atomic absorption spectrophotometry, using techniques described in Cepeda (1986).

Results and Discussion

Lead and copper contents in the soil in the less than 60 mesh fraction at a depth of 30 centimeters are shown in Figures 1 and 2. Data for other mesh fractions and depths are similar to that shown in Figures 1 and 2, although at a depth of 10 centimeters for both Cu and Pb, metal values are not as high and are distributed over a wider area, probably the result of dispersion by southwesterly winds. Contours derived from the data show a rapid decrease in copper content downslope from the dump. Background or near background values are measured approximately 45 meters (150 feet) from the base of the mine dump. Similar results were obtained from copper contaminated soil in the Old Cleora Mining District (Cepeda, 1986), where background values were attained 60 meters downslope from the dumps. However, at Old Cleora, the slope angle was a gentle six degrees in a sandy soil.

Lead contents in the soil remain high all the way down the slope and are more than 50 percent of values in the dump samples at a downslope distance of 76 meters (250 feet), the limit of the slope, before it is intersected by a gravel road. The gravel road marks the base of the slope. At this point it is still well above the background value of approximately 500 parts per million. In contrast, unmineralized Rawley Andesite has a Cu content of 18 to 21 ppm and a Pb content of 21 to 32 ppm (Varga and Smith, 1984). The Bonanza tuff has similar Pb and Cu contents (Varga and Smith, 1984).

The downslope decrease in Pb and Cu values with distance from the dump is depicted graphically in Figure 3. Soil contents of Pb and Cu in this figure have been normalized to the highest value of each metal in

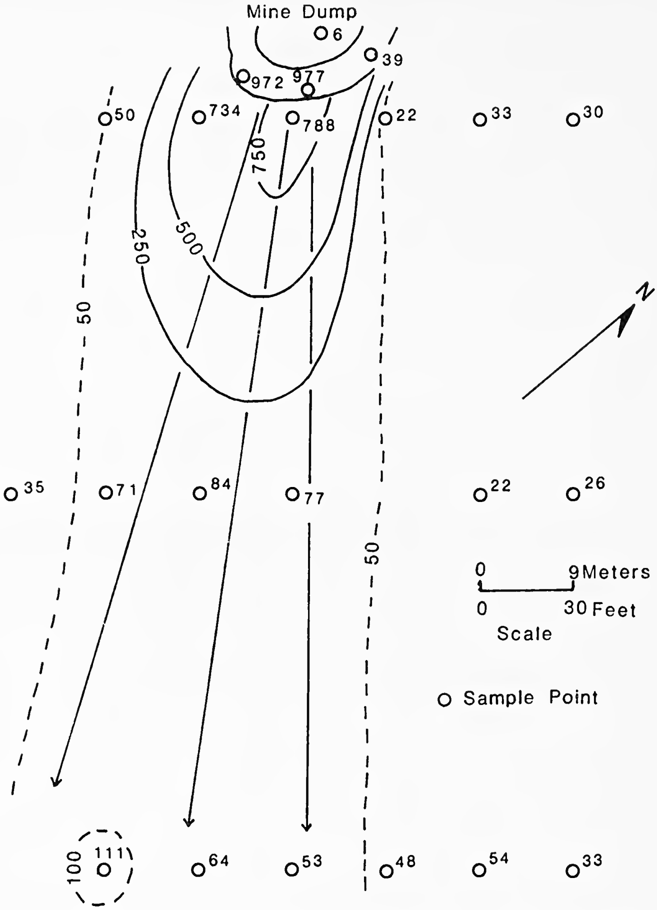

FIGURE 1. Copper concentration (in parts per million) in less than 60 mesh fraction, soil samples at a 30 centimeters depth, Bonanza, Colorado. Arrows indicate downslope direction on 29 degree slope.

the dump. Thus the highest mine dump value is assigned a value of 1.0 and downslope soil metal contents are plotted as a fraction of this highest value. Pb and Cu background values are also shown on Figure 3.

Previous investigators of element mobility in soils have come to mixed conclusions. Several investigations have noted the high mobility of copper in the soil in both a desert (Snoep and Zeegers, 1979) and a humid (Cameron, 1975) environment. Cameron (1975) suggested that the mobility of copper may be due to the high relative solubility of copper sulfate (14.3 grams per 100 milliliters) relative to the lead sulfate (0.004 gm/100 ml). Bogoch and Brenner (1977) noted that lead (and zinc) concentrations in soils adjacent to mineralization in a temperate climate are exceptionally high but downslope and downstream mobility is low.

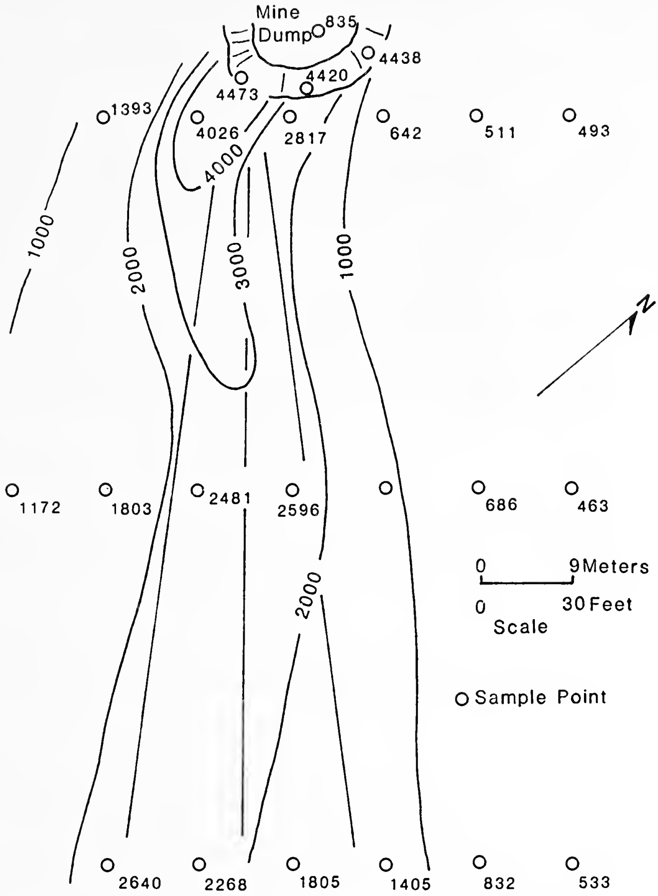

FIGURE 2. Lead concentration (in parts per million) in less than 60 mesh fraction, soil samples at a 30 centimeters depth, Bonanza, Colorado. Arrows indicate downslope direction on a 29 degree slope.

Hoffman and Fletcher (1972) reported a low mobility of copper in an alkaline geochemical environmental in a semiarid climate. In an alkaline environment, the migration of dissolved copper, as copper sulfate, would be inhibited. Hoffman and Fletcher concluded that in such an environment copper gives consistent and meaningful geochemical patterns related to mineralization. This appears to be the case in the Bonanza District where copper exhibits limited mobility in the soil.

The limits of Eh and pH in natural environments (Baas-Becking, 1960) are restricted to a pH between 2 and 10 and an Eh of between −400mV and +800mV. The Eh characteristics of soils and meteoric waters range from about +100 to +700 mV. Measured pH for the Bushvalley soils range from 6.1 to 7.8. Copper species stable in this part of the Eh-pH diagram include chalcocite, native copper, cuprite, and malachite. The

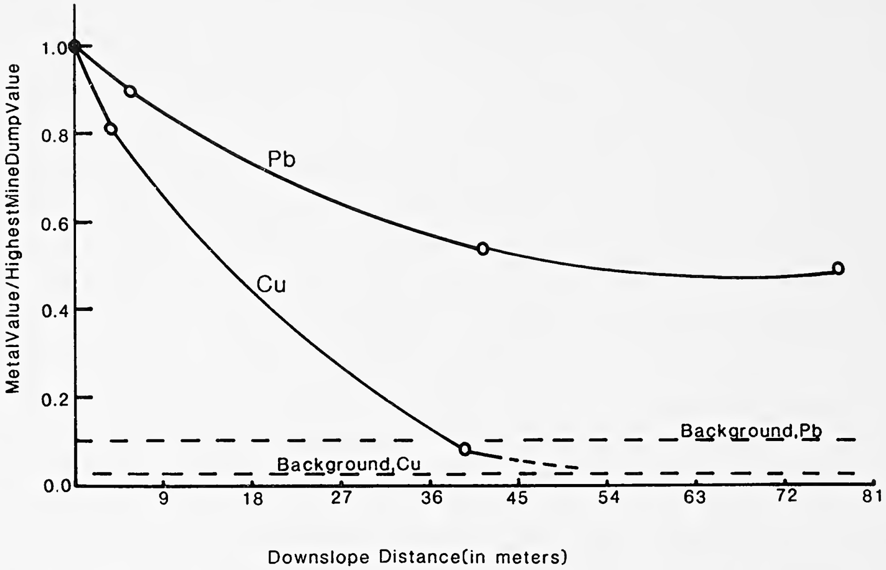

FIGURE 3. Pb and Cu soil contents downslope from mine dump, normalized to highest mine dump value. Highest Pb and Cu values are 4473 and 977 parts per million, respectively. Pb and Cu background values are 500 and 50 parts per million, respectively.

solubility of copper as Cu++ ion in aqueous solution increases with decreasing pH and is approximately 10^{-4} molar at a pH of 6 at 25°C and with $P_{co2} = 10^{-3.5}$ atm (Garrels and Christ, 1965). An increase in pH would promote the precipitation of Cu as malachite or cuprite. A decrease in Eh (more reducing conditions) would favor the precipitation of chalcocite or native copper. A recent study by Hostettler (1984), however, suggested that Eh measurements are difficult to make, and it is not only necessary to consider the effect of minerals but also gases, masses of water, and microorganisms.

CONCLUSIONS

The origin of the dispersion haloes in the Bonanza area, a semiarid climate, is probably due to downslope movement of resistant particles on a steep slope, although it is possible that Cu could be transported in solution. Microscopic examination of panned concentrates of the 30 to 60 mesh fraction of soil reveals metallic sulfide and native copper particles. But indication of relative mobility derived from this study should be utilized with caution because of possible variables such as climate, soil type, pH, Eh, slope, and type of mineralization.

ACKNOWLEDGMENTS

Financial support for the laboratory portion of this project was supplied by a 1981 Organized Research Grant from the Killgore Research Center, West Texas State University, Canyon, Texas. Ron Thomason, Head, Department of Plant Science, kindly allowed use of the department's atomic absorption spectrophotometer and supplied standards for calibration. Trenton Richards assisted the principal investigator in the collection of samples at Bonanza, Colorado. Steve Ritter assisted in laboratory preparation of samples and analytical work. Robert Sawvell provided drafting materials and supplies.

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INFLUENCE OF ENVIRONMENTAL FACTORS ON OXYGEN CONSUMPTION OF *CLIBANARIUS VITTATUS* (STRIPED HERMIT CRAB)

V. A. Wolfenberger
Texas Chiropractic College, Pasadena, Texas 77505

Abstract.—The oxygen consumption of the hermit crab, *Clibanarius vittatus*, was measured under combinations of salinity—10, 20, 30 and 40 parts per thousand, temperature—16, 20 and 24°C, the presence or absence of selenium, and two sites of collection of animals. The general trend was for oxygen consumption by the crabs to increase with increasing temperature. The rate of oxygen consumption tended to decrease with increasing salinities. Selenium depressed the rate of oxygen consumption in animals from the bay environment, whereas erratic results were obtained in animals from the Gulf environment. *Key words*: oxygen consumption; hermit crab; selenium; salinity; temperature.

Oxygen consumption of an organism long has been used as an indicator of stress because it is an indirect measurement of metabolic rate. Various environmental conditions might be expected to produce differing levels of stress in an organism subjected to them. Quantity of oxygen consumption, therefore, would be an indicator of the extent of stress an organism was experiencing.

Four variables were investigated for their influence on the oxygen consumption of *Clibanarius vittatus*, the striped hermit crab. Temperature and salinity are obvious factors that might stress a euryhaline organism. Stress from a pollutant was the third factor. Incorporating two different populations provided crabs that would be expected to show differences in their abilities to adapt to the various conditions included in this study. Interactions or synergistic effects of environmental factors allow a more realistic evaluation of the stress an organism experiences than do single factor evaluations.

The primary purpose of this study was to determine the effects of these environmental factors on the rate of oxygen consumption of the hermit crab, *Clibanarius vittatus*, and to compare these effects in the two populations of the species—one from a bay environment and one from a surf environment.

Clibanarius vittatus is a euryhaline crustacean common in estuarine environments of the Gulf of Mexico. Above a salinity of 20 parts per thousand it maintains its body fluid concentration slightly hyperosmotic to the medium. In more dilute surroundings, it is hyperosmotic to the medium (Sharp and Neff, 1980). Changes in salinity are known to influence oxygen consumption of some crustaceans. However, a sufficient acclimation period occasionally allows return to near-normal oxygen

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consumption rates. Shumway (1978) found that *Pagurus bernhardus* (with shells) increased oxygen consumption sharply when ambient salinity was reduced in 75 percent sea water, either abruptly or gradually, but returned to near-normal oxygen consumption after approximately three hours. Sarojini and Nagabhushanam (1968) found that the oxygen consumption of *Diogenes bicristiamnus* (an Indian hermit crab) decreased with decreasing salinity. Vernberg (1956) reported *Clibanarius vittatus* acclimated to normal sea water consumed 1.28 microliters of O_2 per gram weight per minute. The nonestuarine *Pagurus bernhardus* exhibited withdrawal behavior, cessation of ventilation, and negligible oxygen uptake when exposed to 20.5 to 22.5 parts per thousand salinity (Davenport et al., 1980).

The relationship between temperature and oxygen consumption of poikilothermic organisms such as *Clibanarius vittatus* is often a logarithmic one. Respiratory response to chronic temperature change is less than to acute temperature change; acclimation may occur, resulting in return to near-original rate of oxygen consumption. This return is termed compensation (Precht, 1973). It has not been determined whether *Clibanarius vittatus* compensates or not.

The third ecological factor considered in this study is a pollutant. Some effects of pollutants on respiration in crustaceans have been reported. Exposure for 60 days to mercury at concentrations of 0.5 to 1.0 parts per trillion did not significantly alter the respiratory rate of postlarval *Penaeus setiferus* (Green, et al., 1976). Vernberg et al. (1979) found respiratory rates of *Palaemonetes pugio* exposed to cadmium under static conditions were lower than for nonexposed animals.

The effects of interactions of a pollutant and environmental factors may offer a more realistic means of simulating environmental situations. The synergistic effects of mercury and temperature-salinity on the oxygen consumption of *Uca pugilator* larvae were studied by Vernberg et al. (1973). Mercury depressed the oxygen consumption of the larvae at 25 and 30°C and enhanced oxygen consumption at 20°C. Suboptimal temperature-salinity regimes generally depressed oxygen consumption. The effect of the added stress of mercury was temperature dependent.

The pollution factor considered here is the presence or absence of selenium. Awareness of selenium as a pollutant is increasing. The growing sulfur and petroleum industries are only two of the potential sources of the element on the Texas coast. Geologically, selenium occurs widely and can enter the environment via the weathering of rocks and soils (NAS, 1976). The element also may enter the environment as a result of combustion of fossil fuels (Fleming et al., 1979; Bertine and Goldberg, 1971; Gutemann and Bach, 1976). It also can be a run-off contaminant from soil dressing containing selenium in selenium deficient areas (Gissel-Nielson and Gissel-Nielson, 1973). Inasmuch as selinium tends to accumulate in sediments (Sidelnikova, 1970), dredging operations also might increase available selenium in marine environments.

Several studies have been done concerning the accumulation of selenium by marine organisms. Crustaceans that have been found to accumulate selenimum include the euphausid, *Meganyctiphanes norvegica* (Fowler and Benayoun, 1976a), a shrimp, *Lysmata seticaudata* (Fowler and Benayoun, 1976b), and the water flea, *Daphnia pulex* (Sandholm, 1973).

The fourth parameter to be considered is that of habitat or population effect on physiological response. Whereas several studies have been done comparing populations of invertebrates, not all such investigations have used populations from proximate locations and of the same species. King (1965) reported differences in oxygen consumption of *Callinectes sapidus* from brackish water and from marine waters after acclimation to the same conditions. Loft (1956) found considerable differences in the respiratory rates of two populations of *Palaemonetes varians* as they were subjected to different salinities. The collection sites for the two populations of *Clibanarius vittatus* in this study differed (at least obviously) only in salinity; the bay environment, Steadman's Island, had a salinity range from 12 to 40 parts per thousand, whereas the Gulf-exposed environment ranged from 24 to 35 parts per thousand.

METHODS

This study considers the influence of temperature, salinity and selenium on the oxygen consumption of *Clibanarius vittatus* collected from two habitats near Port Aransas, Texas (Fig. 1). One site, Steadman's Island, is a bay environment to the south of the causeway connecting Aransas Pass and Port Aransas. The second site is on the southwestern shore of Corpus Christi Pass through Mustang Island into Corpus Christi Bay. Animals at this site were collected gulfward from the point at which the Highway P52 bridge crosses the waterway. This area is exposed to Gulf waters, temperatures and salinities.

The animals were transported dry in styrofoam chests to laboratory facilities in College Station, Texas. They were maintained in fiberglass tubs containing 30 parts per thousand artificial sea water at room temperature (approximately 20°C ± 2°C). They were fed Tetra Min ad libitum. No animals were subjected to experimental conditions until they had been in the laboratory a minimum of 10 days, and no animals were used that had been in captivity longer than 90 days. No records were kept of sex. The mean dry weights of the animals from the two collection sites were 1.180506 grams for animals from the Gulf environment and 1.466789 grams for the animals from the bay environment. An F-test (Number Cruncher Statistical System, Version 4.2, 1985) indicated these two means were significantly different at the $\alpha = .05$ level.

Experimental conditions included four salinities, three temperatures, and the presence or absence of a pollutant, selenium. Preparation of animals from each site for experimentation included 96 hours acclimation in three liters of sea water at salinity of 10, 20, 30, or 40 parts per thousand with six to 10 animals per four-quart aquarium. An airstone was placed in each container. These aquaria were kept in an incubator at 16°C, 20°C, or 24°C (all temperatures are ± 1°C) for at least 96 hours prior to performing any experimental tests.

These temperatures and salinities are within the ranges for the Texas coast. A 12-hour, light-dark cycle was maintained. Animals subjected to similar conditions were exposed to the pollutant selenium in the form of sodium selenite. To yield the 100 parts per million

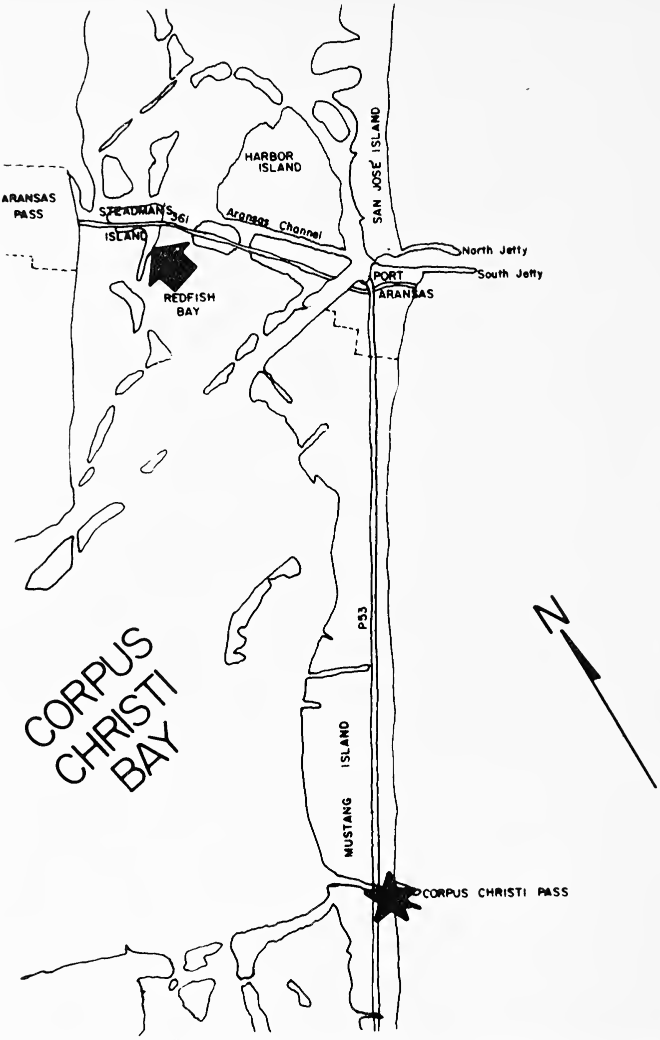

FIGURE 1. Map of the Port Aransas, Texas, area. The bay collection site is indicated by an arrow. The Gulf-exposed collection site is indicated by a star.

exposure concentration of selenium, 0.65714 gram of the compound was added by dissolving the salt in the three liters of sea water 72 hours after acclimation had begun so that the exposure time to the pollutant was 24 hours.

The oxygen consumption of whole animals subjected to experimental conditions was determined. Shells were scrubbed prior to testing. After the 96-hour acclimation period, an animal was placed in a quart container (three-inch inside diameter) containing 502 milliliters of artificial sea water at the acclimation temperature and salinity. A marble was added to facilitate agitation of the water. The sea water had been filtered through a .4 μ Millipore filter to remove bacteria and other microscopic organisms, and it was then vigorously aerated to saturate it with oxygen. Immediately after addition of the animal, a two-milliliter sample of sea water was taken using a glass syringe, which then was sealed. The sea water was covered with eight milliliters of paraffin oil to prevent gas exchange with the atmosphere (Wofford, 1978). The syringes were submerged in an acclimation temperature water bath. The quart containers with animals were kept in an incubator at the acclimation temperature during the test period.

Initial samples of the sea water were analyzed at the acclimation temperatures for oxygen content, using a Radiometer PHM 71 Mk 2 blood gas analyzer that had been modified to maintain constant lower temperatures. At the termination of the experimental period, each container was agitated to disperse diffusion gradients. A second sample was taken by placing the syringe through the paraffin oil; it was analyzed for oxygen content using the Radiometer. The animals were removed from their shells, weighed and dried to a constant weight. An individual animal was tested only once at only one temperature and salinity. Five animals were tested under each set of conditions.

Partial pressures of oxygen were converted to milliliters of oxygen by the equation:

$$\text{ml } O_2/1 = \text{solubility coefficient} \times \frac{\text{mm Hg of sample}}{\text{barometric pressure}} \times (1000)$$

(Giese, 1968). The solubility coefficient in milliliters O_2 per milliliters of water was obtained from Weiss (1970). Measurements of oxygen consumption were made weight specific.

Statistical analysis included multiple analyses of variance (Ott, 1977) incorporating all four factors, as well as multiple analyses of variance performed separately for each site incorporating the other three factors. In instances in which a significant effect attributable to treatment was determined at the $\alpha = .05$ level, multiple linear regression analyses were performed.

RESULTS

The oxygen consumption rates of *Clibanarius vittatus* not exposed to selenium are shown in Figure 2. At 16° C, the oxygen consumption of animals from both sites peaked in 30 parts per thousand salinity at a mean of 6.61 milliliters per milligram per hour for animals from Corpus Christi Pass and of 7.20 for the same measurement for those from Steadman's Island. The instances of lowest rate of oxygen consumption differed between the two sites; for the Pass, the lowest rate occurred in 20 parts per thousand, whereas it occurred in 40 parts per thousand for Steadman's Island animals.

At 20° C, the animals from Corpus Christi Pass had variable rates of oxygen consumption over the range of salinities tested. The rate of oxygen consumption of animals from Steadman's Island at 20° C peaked in 20 parts per thousand salinity and was depressed to 30 parts per thousand. For both sites, the rate of oxygen consumption was usually lower at 20° C than at 16° C.

For Corpus Christi Pass, the oxygen consumption rates at 24° C were higher than for either of the other two temperatures, except the rate at 16° C in 30 parts per thousand was higher than that at 24° C in the same salinity. For animals from Steadman's Island, the rates for all measurements at 24° C were higher than for the other two temperatures at the same salinities. For both sites, the highest mean rate of oxygen consumption was at 24° C in 40 parts per thousand salinity.

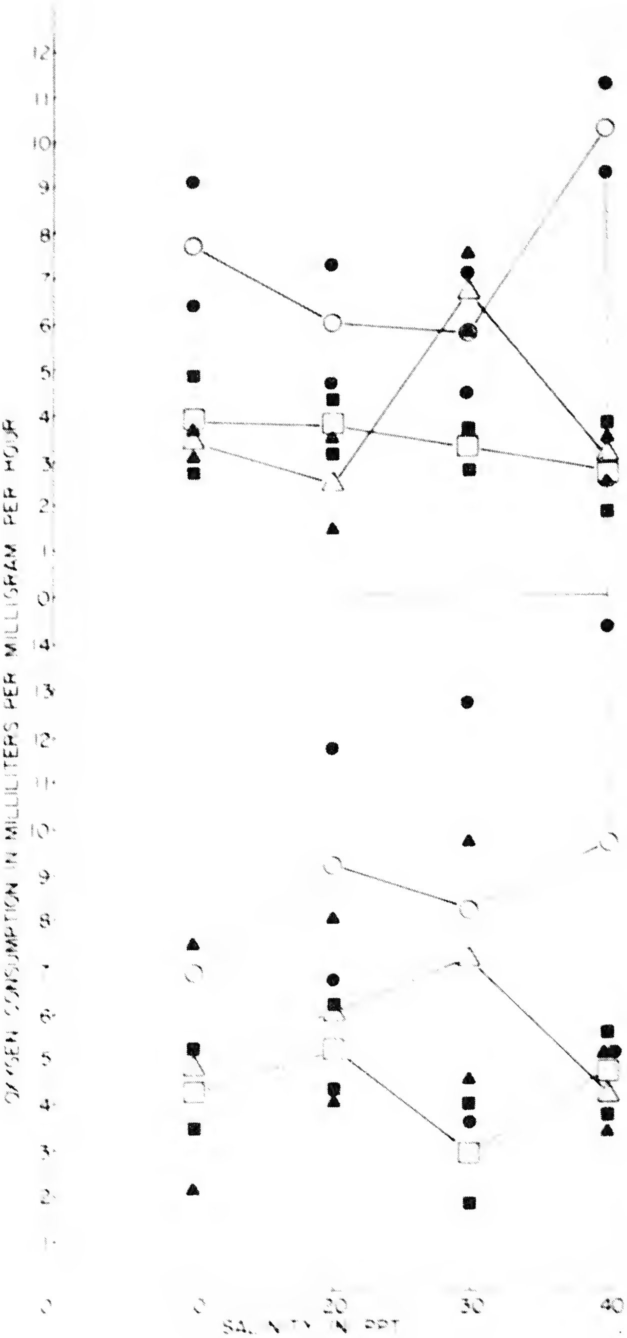

FIGURE 2. Oxygen consumption of whole *Clibanarius vittatus* from Corpus Christi Pass (top) and Steadman's Island, not exposed to selenium. Temperatures are 16° C, △; 20° C, □; and 24° C, ○; standard errors are represented ▲, ■ and ●, respectively. Each open figure represents the mean of five animals.

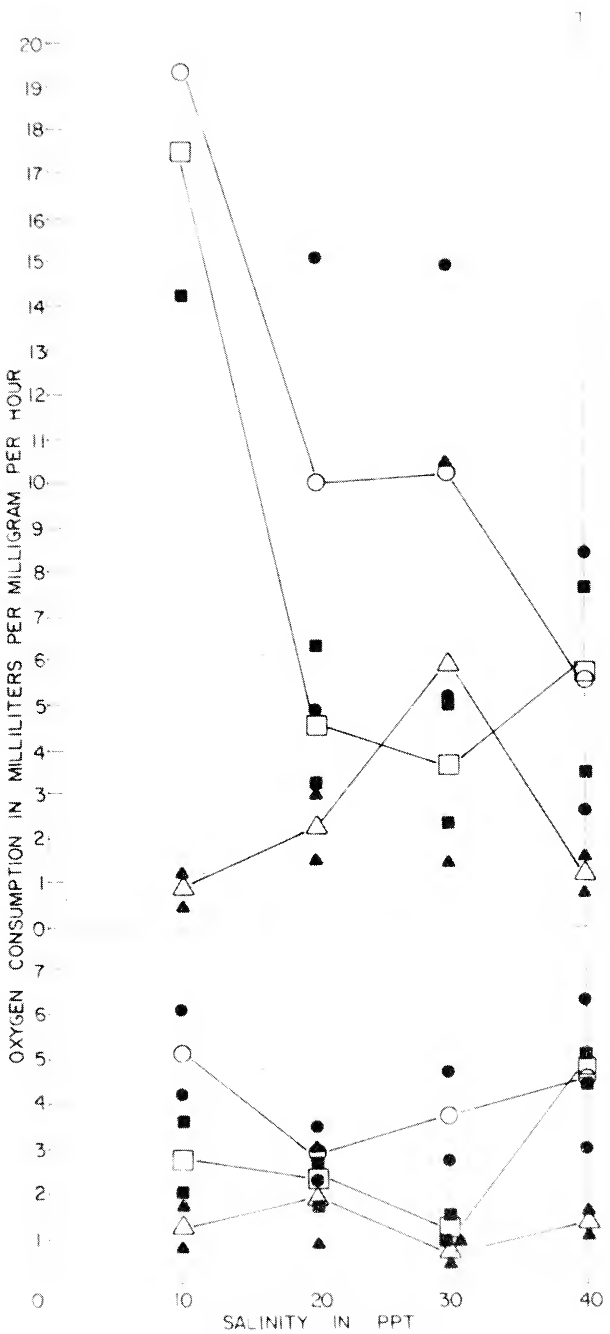

FIGURE 3. Oxygen consumption of whole *Clibanarius vittatus* from Corpus Christi Pass (top) and Steadman's Island, exposed to selenium. Temperatures are 16°C, △; 20°C, □; and 24°C, ○; standard errors are represented by ▲, ■ and ●, respectively. Each open figure represents the mean of five animals.

The pattern of the oxygen consumption rate for crabs exposed to 100 parts per million selenium for Corpus Christi Pass was depressed, but similar to the pattern for nonexposed animals from the Pass (Fig. 3); the point that did not lie in a similar relationship to the other was in 10 parts per thousand at 16°C, which was depressed to 0.87 milliliters per milligram per hour in the selenium-exposed animals; it was 3.34 in the nonexposed animals.

However, rates of oxygen consumption at 20°C were elevated in the selenium-exposed animals in 10 parts per thousand and in 40 parts per thousand salinity, especially in the lower salinity.

At 24°C, oxygen consumption increased greatly in 10 parts per thousand salinities, but these rates were still higher than for the nonexposed animals in similar circumstances. In 40 parts per thousand, however, the rate of oxygen consumption for the selenium-exposed animals decreased to 5.69 milliliters per milligram per hour, but rose in nonexposed animals to 10.22 (Fig. 2).

Responses of animals from Steadman's Island exposed to 100 parts per million selenium were generally lower than for the nonexposed animals. At 16°C, the rates of oxygen consumption did not vary greatly among the four salinities, but they were all lower than any of the rates for similarly treated nonexposed animals.

At 20°C, the exposed hermit crabs displayed a gradual decrease in rate of oxygen consumption for 10 parts per thousand salinity; there was a sharp increase in consumption in 40 parts per thousand. The rate of oxygen consumption in selenium-exposed animals at 24°C was lowest in 20 parts per thousand salinity and increased at both higher and lower salinities, but was still less than the rates for nonexposed animals.

In *Clibanarius vittatus* from Steadman's Island, the rates of oxygen consumption tended to increase with temperature (Fig. 3). The rates of consumption for selenium-exposed animals were higher for Corpus Christi Pass than for Steadman's Island.

An analysis of variance (Table 1) indicated that temperature and site as single factors were influential on the oxygen consumption of the hermit crabs ($\alpha = .05$), but the interactions of selenium and temperature and of selenium and site also were significant.

CONCLUSIONS

The rates of oxygen consumption of *Clibanarius vittatus* from both sites not exposed to selenium were generally higher at 24°C than at the other two temperatures, as would be expected (Kinne, 1964). However, there was also a trend for the rates at 16°C to be greater than those at 20°C. There was apparently an interaction of 16°C and 30 parts per thousand salinity that produced a peak of oxygen consumption for that temperature.

TABLE 1. Analysis of variance of effects of temperature (TEMP), salinity (SAL), selenium (SE) and site on the oxygen consumption of *Clibanarius vittatus*.

Source	DF	SS	F	PR>F
Corrected total	195	4649.778		
Model	30	1826.995	3.56′	
SE	1	19.985	1.17	0.2814
SAL	3	59.880	1.17	0.3241
SE-SAL	3	106.117	2.07	0.1049
TEMP	2	622.124	18.18	0.0001**
SE-TEMP	2	127.244	3.72	0.0263**
SAL-TEMP	6	202.164	1.97	0.0728
SE-SAL-TEMP	6	136.926	1.33	0.2448
SITE	1	104.525	6.11	0.0145**
SE-SITE	1	372.109	21.75	0.0001**
SAL-SITE	3	115.877	2.26	0.0823
TEMP-SITE	2	87.495	2.56	0.0806
Error	165	2822.783		
$R^2 = 0.3929$				

**Significant ($\alpha = .05$).

The lack of influence of salinity on the oxygen consumption of *Clibanarius vittatus* is similar to Shumway's (1978) findings for *Pagurus bernhardus* in that oxygen consumption returned to near-normal rates after acclimation.

The introduction of selenium into the pool of factors did not delete the 30 parts per thousand-16°C peak for animals from Corpus Christi Pass. However, the overall rate at 16°C for the Pass animals was lower than for the nonexposed animals. Generally, rates of oxygen consumption for Corpus Christi Pass selenium-exposed animals increased over those that were not subjected to selenium.

In general, oxygen consumption of estaurine invertebrates increases with decreasing salinity (Kinne, 1964). The overall response to salinity was for these animals to consume less oxygen in 30 parts per thousand than in either higher or lower salinities. This is not surprising because that level often is considered an ambient salinity. The most noticeable exceptions to this were at 16°C. Only animals from Steadman's Island exposed to selenium did not consume less oxygen in 30 parts per thousand than in other salinities, indicating, perhaps, an interaction of 16°C and that concentration of selenium.

The overall increase in rate of oxygen consumption of selenium-exposed hermit crabs from Corpus Christi Pass compared to nonexposed crabs from the Pass versus the overall decrease of oxygen consumption of selenium-exposed animals from Steadman's Island compared to nonexposed animals from the Island was apparently an effect of site, or difference in animal size, inasmuch as the salinity-temperature-selenium regimes were the same for both sites. The two most obvious instances of increase in oxygen consumption at low salinity was of animals from Corpus Christi Pass that were exposed to selenium in 20°C and 24°C, perhaps indicating an interaction of low salinity and selenium for those animals. It is possible that the differences in size of the animals between the two sites had an influence on the oxygen consumed.

The somewhat erratic results on the oxygen consumption of *Clibanarius vittatus* may be explained by the behavior of the animals. There was no way to assure uniform exposure to conditions. The animals had the option of retreating into their own mini-habitats, their shells, to escape the regime imposed on them. This is the most probable explanation of the results obtained for the hermit crabs exposed to 100 parts per million selenium. Shortly after the addition of the compound and its dissolution into the media, the animals became quite active. After approximately two hours, the usual situation upon opening the incubators was to find all animals withdrawn into their shells.

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DIURNAL ACTIVITY PATTERNS OF DESERT MULE DEER IN RELATION TO TEMPERATURE

Bruce D. Leopold and Paul R. Krausman

School of Renewable Natural Resources, University of Arizona, Tucson, Arizona 85721

Abstract.—Desert mule deer (*Odocoileus hemionus crooki*) activity in relation to temperature was studied in Big Bend National Park, Texas. No significant decrease in activity resulting from high temperatures occurred during spring and winter. Summer, and to a lesser extent late summer, activity significantly decreased when air temperature exceeded 33°C.
Key words: activity patterns; desert mule deer; *Odocoileus hemionus*; temperature.

Mammals living in most desert regions evade or counter high temperatures through migration, behavioral (Vorhies, 1945; Bartholomew and Cade, 1957), or physiological adaptations (Taylor, 1969a, 1969b; Schmidt-Nielson, 1959). In North American deserts, however, large ungulates may not have developed physiological mechanisms to counter aridity and high temperatures. Knox et al. (1969) stated that the water kinetics of mule deer do not significantly differ from those of other ruminants. Additionally, preliminary investigations of desert mule deer kidneys collected in southwestern Arizona do not indicate any physiological adaptations to arid environments (Krausman, unpublished data). Desert bighorn sheep (*Ovis canadensis nelsoni*) also lack physiological water conservation mechanisms (Horst, 1971). Thus, desert mule deer may have developed behavioral mechanisms to counter high temperatures and limited available water.

Observations of desert mule deer activity were made in Big Bend National Park, Texas (BBNP), in 1980 and 1981. We analyzed deer activity relative to seasonal changes in temperature patterns to document behavioral responses to temperatures. We hypothesized that desert mule deer were less active during periods of high temperatures compared to periods of low temperature to avoid thermoregulatory stress.

Study Area

BBNP, Brewster County, is located 113 kilometers from Marathon, Texas. The park is characterized by hot summers, mild winters, and low rainfall. Temperatures often exceed 38°C in the desert regions in summer and are rarely as low as freezing in winter. Precipitation occurs primarily from May through October ranging from ≤ 28 centimeters in the desert and the surrounding foothills to 41 centimeters in the mountainous regions.

Two areas in BBNP, Paint Gap Hills and Panther Junction, were studied intensively. The Paint Gap Hills are an igneous intrusion nine kilometers from Panther Junction. Elevations range from 1067 to 1299 meters. Panther Junction is on the flats surrounding the foothills of the northeastern portion of the Chisos Mountains. Elevations range from 884 to 1250 meters.

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MATERIALS AND METHODS

Observations of Deer

Independent deer observations were obtained while hiking the study area. Independent observations were of deer not influenced by another observation nor by the actions of the researcher. Only deer initially observed undisturbed and involved in an activity other than bedded were recorded. Fleeing deer were not included in the analysis. For each observation, we recorded air temperature two meters above ground, time, principal activity when initially observed, age (fawn, yearling, adult), and group size. In addition to the independent observations, activity of free-ranging deer at Panther Junction and Paint Gap were observed from dawn until dusk for 17 days in 1980 and 1981 (spring—seven days, summer—five days, late summer—two days, winter—three days). Total minutes individuals spent feeding, standing, and bedded were recorded. We calculated percent time active (feeding and standing) by pooling individuals. The observation period was from dawn until dusk or when deer moved out of sight during their evening feeding period. Partial observations (not lasting from dawn to dusk) were not included in the calculations. Only adult does were included in the analysis.

Seasonal Activity Assessment

Frequency histograms for the number of deer observed within temperature categories were constructed for each season (spring—February-April, summer—May-July, late summer—August-October, winter—November-January. Sample sizes for each season were relatively equal (spring, 121 days; summer, 107 days; late summer, 110 days; winter, 97 days) thus allowing seasonal comparisons of deer activity. Daily maximum and minimum temperature data were obtained from a weather station at Panther Junction (1140 meters). Contingency table analysis (Zar, 1984) was used to determine differences in frequencies of deer observed within temperature classes between seasons.

RESULTS AND DISCUSSION

Temperature Patterns

Monthly maximum and minimum temperatures at Panther Junction during the study periods ranged from 13.9°C to 37.0°C, and 2.8°C to 23.3°C, respectively. The maximum temperature for June and July was 37.2°C for 1980 and 33.6°C in 1981. The average maximum temperature for June and July from 1960-1979 was 33.9°C.

Seasonal Activity Patterns

In 1980-1981, 749 observations of deer were obtained; however, only 585 observations were of undisturbed deer and subsequently used in the analysis. Deer activity decreased when temperatures exceeded 30°C in summer and 25°C in late summer (Fig. 1). However, similar conclusions regarding activity could be stated for temperatures less than 6°C, but only in winter when temperatures actually fell that low. Diurual temperatures generally reached 33°C in summer and 31°C in late summer within 5 to 7 hours after sunrise. Deer activity decreased when maximum diurnal temperatures were attained. This decrease in activity may have resulted from ambient temperatures approaching or equalling deer body temperature (36-41°C) (Anderson, 1980). Other investigators found similar activity changes by deer in response to diurnal and annual temperature patterns (Clark, 1953; Dasmann and Taber, 1956; Miller, 1970).

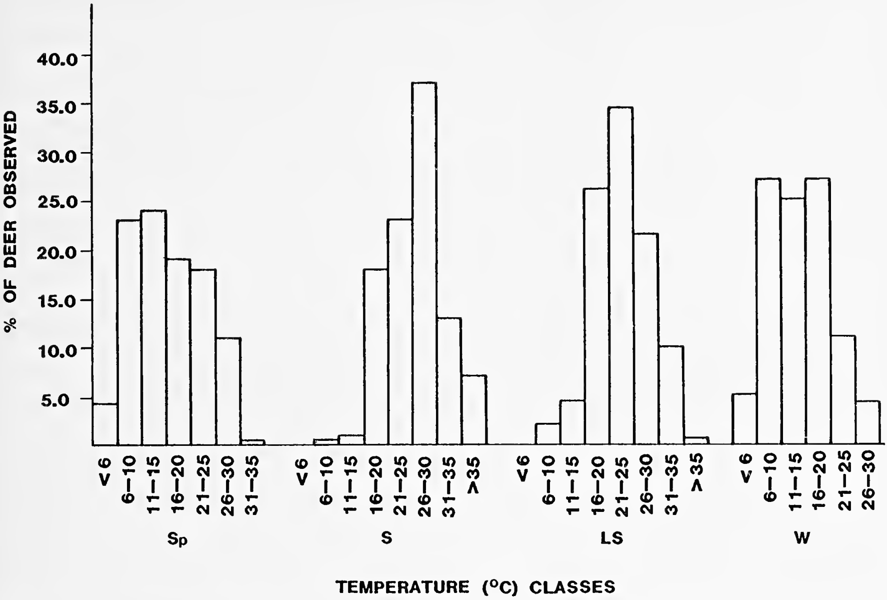

FIGURE 1. Seasonal activity patterns of desert mule deer (DMD) in relation to temperature. (Sp, spring; S, summer; LS, late summer; W, Winter) in Big Bend National Park, Texas, from 1980 to 1981. Numbers on x axis indicate mid-point of temperature class; interval length, 5° C. Total number of observations, 585.

Activity between seasons and temperature classes differed ($P < 0.001$, $X^2 = 255$, df = 15). However, activity in spring and winter did not differ between temperature intervals ($P = 0.134$, $X^2 = 0.843$, df = 5). Colder temperatures during these seasons may have permitted deer to be more active during the day. White-tailed deer (*O. virginianus*) in southern Texas were active 82 percent of the time in winter as compared to 45 percent of the time in summer (Michael, 1970). During the winter in Arizona, desert mule deer spent 60 percent of the day feeding (Clark, 1953). Activity also differed between temperature classes for summer and late summer ($P < 0.001$, $X^2 = 21.8$, df = 4). The significant X^2 was a result of differences in frequencies of deer sightings within temperature classes when temperature exceeded 26° C. Fewer deer were observed in the higher temperature classes during late summer (57 as opposed to 32 percent).

In our study, the percentage of the day spent feeding by adult does increased from spring to winter. Does were active 18 percent of the day in spring (seven days of observation), increasing to 19.7 percent (five days) and 22.7 percent (two days) in summer and late summer, respectively. The highest percentage of the day spent feeding occurred in winter (35.5 percent, three days of observation). This activity may coincide with breeding activities when bucks are actively pursuing does. Twenty-five percent of the movements in winter in the Tucson Mountains, Arizona, was a result of the rut (Clark, 1953). It is more difficult to explain why diurnal activity did not decrease in spring. Spring is the season of lowest rainfall, which may lower the nutritional qualities of forage and cause deer to increase foraging activity to meet their energy requirements.

Also, group size was largest in spring (3.2) compared to other seasons (summer, 2.4; late summer, 2.1; winter, 3.0). Although the number of observations may be the same within temperature categories, the average group size varied seasonally. Michael (1970) found similar results. Dickinson (1978) stated that the only period of significant inactivity in spring was between five and eight hours after sunrise.

Summary and Conclusions

Contrasting the activity patterns of desert mule deer with those of deer studied in more temperate regions (Dasmann and Taber, 1956; Michael, 1970; Miller, 1970), we found that the frequency of deer activity decreased when ambient temperatures reached deer body temperatures. Our observations support our initial hypothesis that observed activity patterns are a behavioral mechanism to avoid temperatures that may result in thermoregulatory stress. However, we realize that measuring temperature without also considering thermal radiation and wind is simplistic in design. Further study is needed to assess these activity patterns in a more comprehensive manner.

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LIMNOLOGICAL CHARACTERISTICS OF AQUILLA LAKE, TEXAS, DURING IMPOUNDMENT

MICHAEL J. MACEINA AND MARY F. CICHRA

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843

ABSTRACT.—Various water chemistry concentrations, as well as phytoplankton, zooplankton, and benthic macroinvertebrate densities were determined for a 14-month period in Aquilla Lake during impoundment. Although large reductions in total phosphorus and chlorophyll *a* levels occurred, and water clarity increased as water volume expanded 10-fold during this period, the reservoir was considered to be eutrophic. Secondarily treated sewage effluent appeared to elevate phosphorus and conductivity concentrations in one arm of Aquilla Lake during the early impoundment phase. As the reservoir filled, however, these higher chemical concentrations were not evident. Regression analysis indicated that 60 percent of the variation in chlorophyll *a* levels was attributable to total phosphorus, total hardness, and to the change in lake volume. Total phosphorus appeared to be the most important parameter regulating algal biomass production. Phytoplankton density changes were not evident with water level increase, but community structure changed over time. Zooplankton abundance was high when compared to other Texas reservoirs. Substrate heterogeneity probably accounted for the differences in abundance of Chironomidae larvae and oligochaetes between the two reservoir arms. *Key words*: total phosphorous; chlorophyll *a*; phytoplankton; zooplankton; benthic macroinvertebrates.

Typically, initial high productivity rates occur at all trophic levels in new reservoirs (Noble, 1980). Nutrient release from newly-flooded soils, detritus, and terrestrial vegetation, and subsequent autotrophic utilization contribute to eutrophy in recently formed impoundments. Over time, reservoir productivity usually declines, but these changes appear to be at least partially dependent on regional geology, hydraulic flushing rates, nutrient input, and sedimentation rates (Baxter, 1977; Canfield et al., 1982; Hoyer and Jones, 1983). However, only limited information pertaining to limnological conditions in newly impounded reservoirs in the western United States has been reported (Mullan and Applegate, 1965; Cooper et al., 1971; Funk and Gaufin, 1971). In Aquilla Lake, Texas, we measured certain physiochemical variables, as well as phytoplankton, zooplankton, and benthic macroinvertebrate densities, to describe limnological conditions in a new Texas reservoir. In addition, nutrient levels were measured in Hackberry Creek, a tributary of the reservoir that receives secondarily treated sewage effluent from the city of Hillsboro, Texas. Temporal variation in limnological variables was examined with respect to impoundment filling. Influence of sewage effluent on water quality also was determined.

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STUDY AREA

Aquilla Lake, a multipurpose U.S. Army Corps of Engineers reservoir in the Brazos River basin, is located in Hill County in east-central Texas (31°55′, 97°10′), approximately 80 kilometers south of Fort Worth (Fig. 1). Impoundment began on 29 April 1983 with water levels reaching conservation pool level (163.9 meters above sea level) on 21 March 1985. At this level, Aquilla Lake has a surface area of 1330 hectares and contains 6450 hectare-meters of water with maximum and mean depths of 15.2 and 4.9 meters, respectively. The dam site, located at the confluence of Aquilla and Hackberry creeks, forms an impoundment containing two large arms, each in a different vegetation region. The Aquilla Arm, located in the Eastern Cross Timbers region, has deep sandy soils with land cover primarily delineated as upland woodlands interspersed with pasture lands (Slack et al., 1986). The Hackberry Arm, located in the Blackland Prairie region, contains alkaline black clay soil with high organic content. Land use surrounding the Hackberry Arm is primarily agricultural cash crops. Secondarily treated sewage effluent is discharged from the city of Hillsboro (population, 7400) approximately five kilometers upstream from the reservoir. The total watershed area above the damsite is 798 square kilometers.

MATERIALS AND METHODS

Limnological samples were collected every other month from six stations on Aquilla Lake between February 1984 and April 1985. Permanent sampling stations were established in February 1985 as the lake approached normal conservation pool (Fig. 1). Prior to this time, stations were located further downstream on the Aquilla and Hackberry Creek arms so that sampling was accomplished in lentic, and not lotic waters. Three stations each were located on the Hackberry and Aquilla Creek arms of the reservoir.

Temperature and dissolved oxygen measurements were taken with a YSI Model 57 oxygen-temperature meter. Water transparency was measured to the nearest five centimeters with a 20-centimeter Secchi disk. Water level readings were obtained from the U.S. Army Corps of Engineers office in Whitney, Texas. Reservoir area and volume determinations were obtained from data provided by the U.S. Army Corps of Engineers (1978).

Surface (0.5 meter) water samples were collected in acid-washed, one-liter Nalgene sampling bottles and placed on ice for analysis the next day in the laboratory. Lake pH was determined with a Cole-Palmer pH meter calibrated with standard buffers of pH 7.0 and 10.0. Conductivity was measured with an Electronic Switchgear Mark IV Conductivity Measuring Bridge standardized to 25°C. Total hardness, total alkalinity, nitrate-nitrite, ammonia, and organic nitrogen and total phosphorus concentrations were determined utilizing the procedures presented by Hach Chemical Company (1979). Total nitrogen was considered to be the sum of nitrate-nitrite, ammonia, and organic nitrogen. Total nitrogen to total phosphorus ratios were computed using weight concentrations.

In September 1984, the effluent discharge rate (cubic meters per second) from the City of Hillsboro sewage treatment plant into Hackberry Creek was estimated and water samples were collected approximately two kilometers downstream from the discharge. Flow in Hackberry Creek during dry conditions in August and September was due entirely to plant discharge. During this time, discharge from Aquilla Creek was nil with intermittent, stagnant pools found along the creek bottom. Total phosphorus and nitrogen levels were determined in the laboratory and daily and annual nutrient loading rates from effluent discharge were derived for Aquilla Lake. Unpublished water chemistry data were provided by the U.S. Geological Survey.

To determine chlorophyll *a* values, a known volume of water was filtered through a 12.5-centimeter Gelman GF/A glassfiber filter that retained particles larger than 0.3 μ meters. Samples were frozen in a dessicator dish with analysis and calculations performed according to standard methods (A.P.H.A., 1976). Chlorophyll *a* values were not corrected for pheophytin. To determine the composition of the phytoplankton community, a single surface

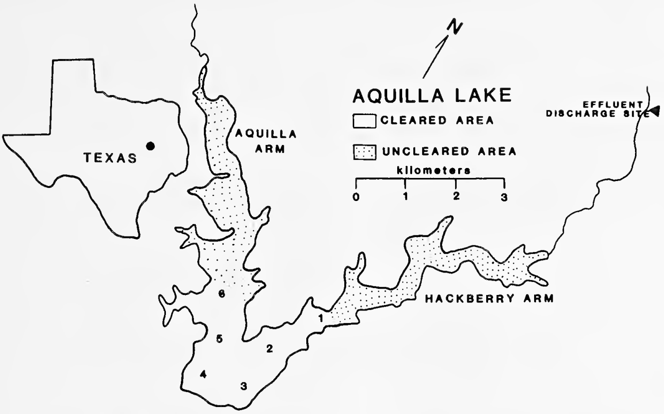

FIGURE 1. Location and map of Aquilla Lake. Numeric values represent limnological sampling stations. Normal conservation pool elevation is 163.9 meters above sea level.

(0.5 meter) 200-milliliter water sample was collected at each station and preserved in buffered Lugol's solution. In the laboratory, a 10-milliliter aliquot from each sample was settled for 24 hours, and examined on an inverted microscope at ×400. Phytoplankton were identified and enumerated in randomly selected strips until the count of the most abundant taxon approximated 100 (Lind, 1974). Keys used for identification were Prescott (1978) and Whitford and Schumacher (1984).

Zooplankton were collected using a 153-μ meter Wisconsin plankton net. Triplicate vertical tows were taken from the reservoir bottom to the surface. When water depth exceeded five meters, tow distance was 5.0 meters. Samples were preserved in five percent formalin-rose bengal solution. In the laboratory, a 5.0-milliliter sample was placed on a Ward circular wheel, and zooplankton were identified, and counted using a binocular dissecting scope at ×30-×60. Cladocerans were identified to genus when possible using the keys provided by Pennak (1978). Calanoids, cyclopoids, copepod nauplii, and rotifers were enumerated as such. Zooplankton counts were converted to concentrations (numbers per cubic meter) assuming 100 percent net efficiency.

Triplicate benthic samples were collected at all stations with a 232 square centimeter Ponar dredge and preserved in a 10 percent formalin-rose bengal solution. Samples were washed in a U.S. Standard no. 30 seive, and organisms removed and placed in 70 percent ethanol. Organisms were counted under a binocular dissecting microscope at ×20 and identified to the most practical taxonomic group using the keys of Pennak (1978) and Merritt and Cummins (1978).

Data were analyzed using the statistical procedures published by the SAS Instutute Inc. (1985). Unless otherwise stated, statistical significance is defined as $P < 0.05$. Mean values for certain data ranged over several orders of magnitude and the variances were proportional to the means. Log_{10} transformation of these data was performed and geometric means were computed. Unless otherwise stated, however, mean values represent arithmetic means. Duncan's multiple range tests and t-tests were used to test differences among and between mean values.

RESULTS AND DISCUSSIONS

Physiochemical Parameters

Temperature and oxygen profiles indicated that Aquilla Lake is a warm monomictic reservoir (Wetzel, 1975). Oxygen stratification was evident

TABLE 1. Mean, standard deviation, minimum, and maximum values for water chemistry parameters, chlorophyll *a*, and secchi disk readings collected from Aquilla Lake, February 1984 to April 1985.

Parameter	Mean	Standard deviation	Minimum	Maximum
pH	8.2	0.5	7.5	9.1
Conductivity (μS)	600	140	440	980
Total hardness (mg.L^{-1} as $CaCO_3$)	140	10	120	170
Total alkalinity (mg.L^{-1} as $CaCO_3$)	140	20	100	180
Total nitrogen (mg.L^{-1} as N)	2.29	1.78	0.28	7.13
Total phosphorus (mg.L^{-1})	0.16	0.26	0.01	0.91
Chlorophyll *a* (mg.m^3)	31	19	1.9	107
Secchi (cm)	50	15	20	85

during the summer 1984, however, maximum thermal variation in the water column was only 1.5° C. Thermal stratification probably did not occur in summer months due to wind mixing in this shallow lake. Between June and August 1984, mean depth was only 2.7 meters.

During the study period, water quality parameters were highly variable (Table 1). Based on pH, total hardness, total alkalinity, and conductivity values, Aquilla Lake is moderately hard-water, well-buffered reservoir with a high mineral content. Mean total phosphorus (TP), total nitrogen (TN), and chlorophyll *a* (Chl*a*) concentrations indicate that Aquilla Lake is highly eutrophic according to criteria established by Forsberg and Ryding (1980). These authors classified lakes as eutrophic when TP, TN, and Chl*a* concentrations exceeded 0.025 milligrams per liter, 0.60 milligrams per liter, and seven milligrams per cubic meter, respectively. The Trophic State Index (TSI) values described by Carlson (1977) for TP, Chl*a*, and secchi disk readings were 77, 64, and 70, respectively, indicating that Aquilla Lake is eutrophic. TSI values are scaled from 0 to 100, where 0 represents extreme oligotrophy and 100 is hypereutrophy.

Temporal water quality changes were apparent during the study period (Fig. 2). Lake pH levels declined from 8.8 to 9.0 in early 1984 to 7.6 to 8.3 by late 1984-early 1985. Conductivity readings generally declined from a high of 930 μS in February 1984 to 560 μS in April 1985. Total hardness fluctuated somewhat during the 14 month period, however, large changes were not observed. TN increased from a mean concentration of 0.50 milligrams per liter August 1984 to 4.56 milligrams per liter in December 1984. Mean TP concentrations declined from 0.78 milligrams per liter in February 1984 to 0.03 milligrams per liter in April 1985.

Changes in many water chemistry parameters appeared to be influenced by increases in water level. Reservoir area increased from 309 hectares to 1359 hectares and volume from 664 hectare-meters to 6730 hectare-meters during this study (Fig. 2). Conductivity, TP, and total alkalinity were negatively correlated with the increase in reservoir area (Table 2).

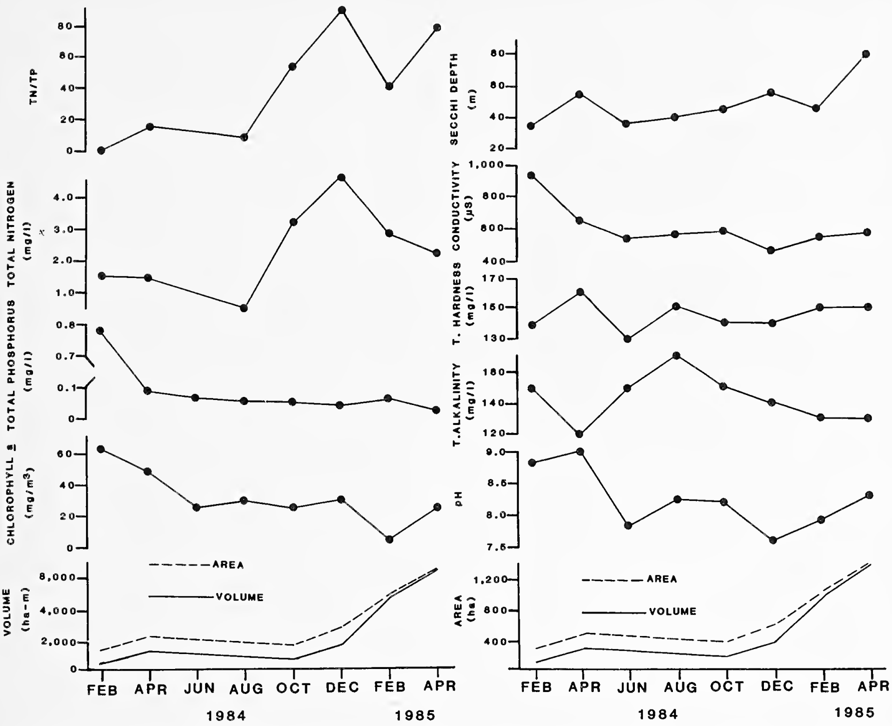

FIGURE 2. Water chemistry concentrations, chlorophylla *a*, and secchi disk depth changes in Aquilla Lake compared to changes in lake volume and area.

Water level increases probably caused reductions in conductivity and TP concentrations due to dilution. Nitrate-nitrite was positively correlated with water level and volume. Newly flooded terrestrial vegetation possibly elevated nitrate-nitrite concentrations as decomposition occurred. Funk and Gaufin (1971) reported elevated nitrate-nitrogen levels after inflow of runoff water in a new Wyoming reservoir. Leaching from the watershed also may account for variation in chemcial concentrations over time.

Mean conductivity and TP concentrations were higher in the Hackberry Arm than in the Aquilla Arm in February and April 1984 (Table 3). After April 1984, when water levels increased, conductivity and TP levels were relatively similar between arms although some significant differences were observed in December and February 1984-85. Higher TP and conductivity concentrations measured in the Hackberry Arm in early 1984 when Aquilla Lake water level was low, may be due in part to sewage effluent. Based on a discharge rate of 0.0375 cubic meters per second and a TP concentration of 0.96 grams per cubic meter, as measured in September 1984, the annual phosphorus loading rate into Aquilla Lake from the Hillsboro sewage treatment plant was computed to be 1130 kilograms. This value assumes a discharge rate of 1.2×10^6 cubic meters per year, which

TABLE 2. Pearson product-moment correlation coefficients relating water quality parameters, chlorophyll *a* concentration, and secchi disk readings to change in lake area and volume in Aquilla Lake.

	Aquilla Lake	
Parameter	Area (ha)	Volume (ha-m)
Conductivity	−0.33*	
Total phosphorous	−0.39**	−0.34*
Total alkalinity	−0.51**	−0.50**
Nitrate-nitrite	0.76**	0.75**
Chlorophyll *a*	−0.49**	−0.46**
Secchi	0.66**	0.65**

$*P<0.05$, $**P<0.01$

was similar to rates reported by the U.S. Geological Survey (1983). Assuming no sedimentary loss of phosphorus and a hydraulic flushing rate of one year, effluent input would elevate TP concentrations in Aquilla Lake approximately 0.02 milligrams per liter. This TP level is comparable to reservoir concentrations measured in April 1985. Water chemistry data collected between February 1984 and April 1985 on Hackberry Creek indicated average TP concentration was approximately 17 times higher below the effluent discharge site than above (U.S. Geological Survey, unpublished data). Hence, Hackberry Creek probably will serve as a major source of phosphorus in Aquilla Lake, although some sedimentary phosphorus loss can be expected (Vollenweider, 1969). In addition, conductivity, sodium, postassium, chloride, total dissolved solids, and TN levels were higher in Hackberry Creek below the effluent discharge site when compared to concentrations collected above the site (U.S. Geological Survey, unpublished data). Thus, higher conductivity readings measured in the Hackberry Arm in early 1984 may have been due to sewage discharge. In September 1984, TN concentration was 12.5 grams per cubic meter below the effluent discharge site on Hackberry Creek with a computed annual loading rate of 14,800 kilograms of nitrogen. TN differences between arms, however, were not evident. This suggests that nitrogen assimilation or loss occurred before reaching the first upper Hackberry Arm station, which is 11 kilometers downstream from the discharge site. Differences in soil types, as well as land use practices between Hackberry and Aquilla creeks also may have influenced nutrient and chemical concentration in the reservoir. The rapid rise in water levels probably negated some of the water quality differences that might have been observed between arms.

During this study period, water clarity in Aquilla Lake generally increased from a mean Secchi disk reading of 25 to 80 centimeters (Fig. 2). Pearson product-moment correlation analysis indicated a significant positive relationship (r = 0.66) between Secchi disk readings and reservoir area during the study period (Table 2). Only a weak (P =0.09) negative relationship ($r = -0.24$) was observed between Secchi disk readings and Chl*a* levels. Generally, higher Chl*a* concentrations reduce water clarity in lakes (Canfield and Bachmann, 1981). Increases in water clarity associated with rising water levels probably were caused by dilution and a reduction of clay turbidity due to addition of organic material. In addition, the increase in mean depth may have resulted in less sediment disturbance. During the study period, mean depth increased from 2.0 to 4.9 meters. Wind related turbidity is usually greater in shallow lakes. Thus, higher water levels might have reduced the effects of wind on water clarity.

Phytoplankton

Chl*a* concentrations, a measure of phytoplankton biomass, averaged 31 milligrams per cubic meter during the study period (Table 1). However, concentrations were highly variable as individual station values ranged from 1.9 to 107 milligrams per cubic meter. Peak Chl*a* levels were observed in February 1984, averaging 62 milligrams per cubic meter, and declined to 25 to 30 milligrams per cubic meter in summer-autumn of 1984 (Fig. 2). Reservoir volume increased 147 percent between December 1984 and February 1985 while mean Chl*a* values declined from 29 to four milligrams per cubic meter; however, mean concentration increased to 25 milligrams per cubic meter by April 1985. Chl*a* was positively correlated ($r = 0.68$, $P < 0.01$) to TP and also positively, but weakly correlated ($r = 0.27$, $P = 0.05$) to total hardness concentrations. Log_{10}Chl*a* levels were negatively correlated ($r = -0.45$, $P < 0.01$) to water volume changes in the reservoir. The multivariate regression equation was computed:

$$\mathrm{Chl}a = -69.0 + 49.1\ \mathrm{TP} + 0.66\ \mathrm{THARD} - 0.055\ \mathrm{CHAVOL}$$

where Chl*a* = chlorophyll *a* concentration in $\mathrm{mg.m^{-3}}$
TP = total phosphorous in $\mathrm{mg.L^{-1}}$
THARD = total hardness in $\mathrm{mg.L^{-1}}$
CHAVOL = the percent change in lake volume.

This equation was highly significant ($P < 0.01$) as these three variables explained 60 percent ($r^2 = 0.60$) of the Chl*a* variation during the study period. The variables, TP, THARD, and CHAVOL, explained 46, 11, and three percent of Chl*a* variation, respectively. These data indicate that TP was the most important parameter affecting Chl*a* concentrations. Analogous with greater TP concentrations, significantly higher Chl*a* levels were observed in the Hackberry Arm in February and April 1984 (Table 3).

Turbidity, dissolved solid concentrations, and other nutrients, such as TN, also effect Chl*a* levels in lakes (Baxter, 1977; Hoyer and Jones, 1983). The mean TN:TP ratio was highly variable during the study period ranging

TABLE 3. Mean water quality concentrations in Hackberry and Aquilla arms at Aquilla Lake.

		1984						1985	
Parameter	Arm	Feb	Apr	Jun	Aug	Oct	Dec	Feb	Apr
Conductivity (μS)	Hackberry	970 *	740 *	530	560	600	460	590 *	570
	Aquilla	890	550	540	540	570	440	520	560
Total phosphorous (mg.L^{-1})	Hackberry	0.88 *	0.13 *	0.12	0.07	0.07	0.06 *	0.06 *	0.03
	Aquilla	0.69	0.06	0.02	0.04	0.06	0.05	0.09	0.02
Chlorophyll *a* (mg.m^{-3})	Hackberry	80 *	52 *	27	27	25	32	5.0	26
	Aquilla	43	44	23	33	24	26	3.9	25

*t-test indicates higher mean value is significantly ($P<0.05$) greater than corresponding lower mean value for a particular sampling date.

from 1.3 to 91 (Fig. 3). When TN:TP ratios are less than 10, TN becomes limiting to algal production (Sakamoto, 1966). This was evident between February 1984 and August 1984. When TN:TP ratios are between 10 and 17, either nutrient can be limiting. When the ratio exceeds 17, TP is generally considered to limit phytoplankton production. The TN:TP ratio was greater than 17 between October 1984 and April 1985 suggesting TP limitation. Regression analysis indicated TP to be the most important parameter regulating Chl*a* levels. Therefore, as Aquilla Lake reached conservation pool level, phosphorus appeared to be limiting algal biomass production. Stauffer (1985) also reported higher phytoplankton production in lakes that had greater calcium carbonate concentrations. Our regression model suggests total hardness was a moderately important parameter regulating Chl*a* levels in Aquilla Lake. Rapid increase in lake volume affected Chl*a* directly by dilution of the phytoplankton community and indirectly by reducing TP levels in the lake.

Total phytoplankton abundance was highly variable as geometric mean densities ranged from 1.73×10^3 cells per milliliter in June 1984 to 7.04×10^3 cells per milliliter in October 1984 (Table 4). Chl*a* concentration was only moderately correlated ($r = 0.32$, $P = 0.03$) to total phytoplankton density. Cellular Chl*a* content can be highly variable among different phytoplankton taxa (Canfield et. al., 1985), which probably accounted for this weak relationship. Phytoplankton community structure changed over time as chlorophytes dominated the flora in February 1984. At this time, *Chlamydomonas* and *Ankistrodesmus* numerically comprised 70 percent and 24 percent of the plankton flora, respectively. *Cyclotella* chains were the predominant algal form in April 1984 (43 percent), December 1984 (36 percent), and February 1985 (73 percent). In April 1985, *Cyclotella*

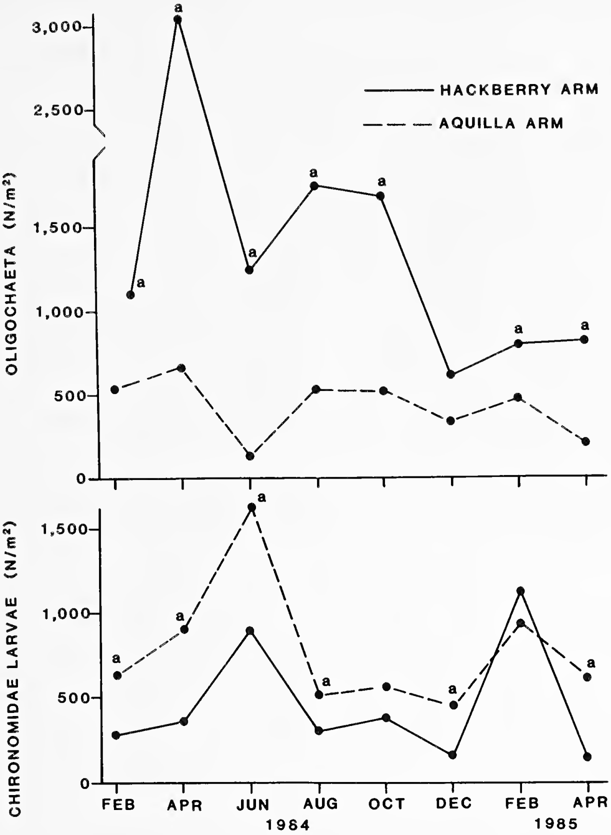

FIGURE 3. Mean Oligochaeta and Chironomidae larvae densities between Aquilla and Hackberry arms. The "a" indicates the higher mean value is significantly ($P < 0.05$) greater than the lower mean value for a particular sampling date.

singles comprised 80 percent of the phytoplankton community. *Nitzchia* and *Melosira* diatoms also were numerically abundant during peak Chrysophyta densities. The cyanophytes, *Raphidiopsis* and *Oscillatoria*, were the predominant algae collected in August 1984 (31 and 40 percent, respectively) and in October 1984 (42 and 30 percent, respectively). Changes in total phytoplankton density were not evident with water level increase, although seasonal as well as water level increase appeared to alter phytoplankton community structure.

Invertebrates

Five major genera of Cladocera (*Daphnia, Bosmina, Ceriodaphnia, Diaphanosoma,* and *Chydorus*) were collected from Aquilla Lake during the study period. Other cladoceran genera that were identified, but the low abundance of which prevented statistical analysis, included *Alona, Alonella*, and *Pleuroxus*. Chronological differences in *Daphnia* abundance

TABLE 4. Geometric mean density (number per milliliter) of major phytoplankton classes in Lake Aquilla. Geometric mean values in columns followed by the same letter are not significantly ($P > 0.05$) different.

	Taxon			
Month	Chlorophyta	Cyanophyta	Chrysophyta	Total phytoplankton
1984				
Feb	4369^a	23^c	60^c	4635^b
Apr	1002^b	35^c	2790^a	4439^b
June	280^d	236^b	791^b	1727^d
Aug	217^d	3954^a	656^b	5254^{ab}
Oct	819^b	5419^a	513^b	7036^a
Dec	461^c	123^b	2325^a	3132^c
1985				
Feb	327^{cd}	1^d	2382^a	2802^c
Apr	249^d	0^d	4747^a	5248^{ab}

were evident as greatest mean density occurred in April 1984 (Table 5). *Daphnia* declined during the summer months, then increased between October 1984 and April 1985. Significantly lower numbers of *Daphnia* were collected in April 1985 than in April 1984, however, no differences were observed between February sampling dates. *Bosmina* displayed similar temporal differences as peak abundance occurred in February and April 1985. *Bosmina* density was significantly higher in February 1985 when compared to February 1984. Differences were not observed between April sampling dates. Maximum *Diaphanosoma* abundance occurred in June 1984, then declined during winter and spring 1985. *Ceriodaphnia* density was extremely low between February and August 1984, but increased in late 1984. *Ceriodaphnia* peaked in April 1985 and this organism became the dominant cladoceran in the lake. *Chydorus* was relatively abundant in early 1984, however, few of these organisms were collected after that time.

The rapid increase in water levels that occurred in early 1984 and early 1985 did not appear to reduce total cladoceran density. The density of Cladocera was significantly higher in April 1984 as compared to April 1985 (Table 5); however, Cladocera abundance in February 1985 was greater than that observed in February 1984. *Chydorus*, which is a small, shallow-water, littoral cladoceran (Pennak, 1978), appeared to be negatively affected by increase in water level. During the study period, mean depth increased from 2.0 to 4.9 meters and pelagic sampling stations were deeper by the end of the study. Thus, a reduction in the open-water *Chydorus* populations might be expected. The zooplankton community was not sampled in shallow water where higher *Chydorus* densities possibly occurred.

Maximum calanoid, cyclopoid, and nauplii Copepoda density occurred in April 1984 (Table 6). Abundance declined in summer and autumn of

TABLE 5. Geometric mean density (number per cubic meter) of Cladocera zooplankton collected in Aquilla Lake. Geometric mean values in columns followed by the same letter are not significantly ($P > 0.05$) different.

	Taxon					
Month	*Daphnia*	*Bosmina*	*Diaphanosoma*	*Ceriodaphnia*	*Chydorus*	Total Cladocera
1984						
Feb	5500^b	200^b	0^e	0^e	130^b	7700^e
Apr	$80{,}220^a$	$18{,}300^a$	0^e	4^d	5700^a	$111{,}000^a$
Jun	23^d	190^c	$10{,}700^a$	3^d	2^{cd}	$12{,}300^d$
Aug	120^c	4^c	4700^b	4^d	0^d	5500^f
Oct	4300^b	220^b	4100^{bc}	2300^b	1^{cd}	$13{,}300^d$
Dec	6400^b	$12{,}300^a$	2200^{bc}	2800^b	0^d	$25{,}300^c$
1985						
Feb	3600^b	$21{,}200^a$	9^d	310^c	4^c	$26{,}500^c$
Apr	6600^b	$20{,}900^a$	1800^c	$30{,}800^a$	0^d	$62{,}900^b$

1984, but generally increased between December 1984 and April 1985. Nauplii density declined significantly in April 1985 when compared to April 1984, but a difference was not apparent for February sampling dates. Similarly, calanoid and cyclopoid numbers were significantly lower in April 1985 than in April 1984. Greater numbers of calanoids were collected in February 1985 when compared to 1984, but cyclopoids were less abundant in February 1985 when compared to mean density one year earlier. Total copepod density was two-fold and five-fold lower in February and April 1985 when compared to corresponding months in 1984. Rotifers, which included the genera *Asplanchna, Polyarthra, Hexarthra, Keratella, Conochilus,* and *Brachionus*, declined dramatically during the study period (Table 6). Peak rotifer abundance occurred in April 1984. A 25- to 50-fold reduction in rotifer density was observed when compared to data collected in early 1984. Similarly, total zooplankton abundance was highest in April 1984. Lowest densities were recorded in summer 1984 and gradually increased from October 1984 to April 1985 (Table 6).

In Aquilla Lake, the annual mean density of zooplankton collected from February to December was 125 organisms per liter. This density was considerably higher than that reported for six Texas reservoirs, where average annual densities ranged from 22 to 60 organisms per liter as reviewed by Cichra et al. (1985). High levels of allochthonous and autochthonous organic material probably were present during reservoir filling and impoundment. This material, in addition to relatively high Chl*a* concentrations, provided ideal conditions for zooplankton population expansion in Aquilla Lake.

Although water levels increased in early 1985, chronological reductions in copepods and rotifers may not have been directly due to this factor. Between February and April 1984 reservoir area and volume increased 65

TABLE 6. Geometric mean density (number per cubic meter) of Copepoda, Rotifera, and total zooplankton collected in Aquilla Lake. Geometric mean values in columns followed by the same letter are not significantly ($P > 0.05$) different.

	Taxon					
Month	Copepods nauplii	Calanoida	Cyclopoida	Copepoda	Rotifera	Total zooplankton
1984						
Feb	1300^{bcd}	1900^{e}	42,000^{b}	46,300^{b}	51,200^{b}	107,000^{b}
Apr	14,900^{a}	36,900^{a}	174,000^{a}	232,000^{a}	111,000^{a}	459,000^{a}
Jun	140^{e}	2100^{e}	2200^{e}	5300^{f}	1900^{d}	20,200^{e}
Aug	130^{cd}	5500^{d}	2400^{e}	9300^{e}	4700^{c}	23,200^{e}
Oct	460^{d}	8600^{c}	4100^{d}	14,500^{d}	2100^{d}	30,700^{d}
Dec	2800^{b}	8100^{c}	11,300^{c}	22,900^{c}	4200^{c}	53,200^{c}
1985						
Feb	1700^{bc}	10,700^{bc}	10,300^{c}	24,600^{c}	2000^{d}	55,200^{c}
Apr	2100^{bc}	19,000^{b}	16,500^{c}	43,400^{b}	2100^{d}	113,000^{b}

and 125 percent, respectively. Maximum zooplankton abundance occurred in April 1984 indicating the change in reservoir area did not reduce zooplankton density. Between December 1984 and February 1985, lake area and volume increased 73 and 147 percent. Although many other variables may be involved in regulating zooplankton abundance and composition, reduction in Chl*a* levels possibly was an important factor in the decline in zooplankton. In February and April 1984, Chl*a* averaged 55 milligrams per cubic meter. One year later, average Chl*a* concentration for the same time period was 15 milligrams per cubic meter. Correlation analysis indicated cyclopoids ($r = 0.44$), rotifers ($r = 0.55$) and total zooplankton abundance ($r = 0.40$) all were positively, but weakly, correlated with Chl*a* levels. Higher Chl*a* levels during this time period would be advantageous to herbivorous zooplankton. Noonan (1979) reported a positive relationship ($r = 0.51$) between total zooplankton abundance and Chl*a* in natural and artificial midwestern temperate lakes. Canfield and Watkins (1984) also found a positive correlation ($r = 0.66$) between Chl*a* and zooplankton in natural Florida lakes. Short term variation in zooplankton density, as well as selective grazing by fish and invertebrate planktivores, also may have affeted the zooplankton community in Aquilla Lake. Spatial differences in zooplankton abundance were not evident during the study period.

Predominant benthic macroinvertebrates collected were Oligochaeta and Diptera larvae, including Chironomidae and *Chaoborus* (Table 7). Comparison of geometric mean densities for pooled data between arms indicated chironomids to be three times more abundant in the Aquilla Arm. Oligochaeta density was four times higher in the Hackberry Arm. Nondipteran immature insects, including Ephemeroptera, Trichoptera, and Odonata, were numerically more abundant in the Aquilla Arm (Table 7).

TABLE 7. Geometric mean density (number per square meter) of dominant macroinvertebrates collected from the Hackberry (stations 1-3) and Aquilla (stations 4-6) arms, February 1984 to April 1985. Nondipteran Insecta include immature Ephemeroptera, Trichoptera, and Odonata.

Taxon	Arm		
	Hackberry		Aquilla
Chironomidae larvae	185	*	540
Chaoborus larvae	6	*	13
Nondipteran Insecta	1	*	3
Oligochaeta	771	*	170
Total benthic invertebrates	1462	*	1157

*t-test indicates higher mean value is significantly ($P < 0.05$) greater than corresponding lower mean for a particular taxon.

Seasonal and spatial density differences were evident as chironomids were found in greater numbers in the Aquilla Arm for six out of eight sampling dates (Fig. 3).

Substrate differences probably account for benthic macroinvertebrate heterogeneity between arms in Aquilla Lake. Correlation between bottom oxygen concentrations and benthic organism density was not evident. The predominantly clay substrate in the Hackberry Arm provides suitable burrowing habitat for aquatic oligochaetes (Wetzel, 1975). Nondipteran Insecta in this study, with the exception of *Hexagenia*, all inhabit the bottom substrate surface. The harder bottom type in the Aquilla Arm may be more suitable to these organisms. Although oligochaete and chironomid densities appeared generally to decline during the study period (Fig. 3), significant differences were not evident. Therefore, impact of rising water levels on these organism was not apparent.

CONCLUSION

Although reductions in TP and Chl*a* concentrations occurred as Aquilla Lake filled, the reservoir was considered eutrophic during the entire impoundment period. Spatial differences for some chemical and Chl*a* levels were evident early in the impoundment phase. Secondarily treated sewage effluent from Hackberry Creek appeared to cause TP and conductivity concentrations to be higher in the Hackberry Arm during the early phase of impoundment. After this time, however, rising water levels probably negated water quality differences between arms. The hydraulic flushing rate in Aquilla Lake is predicted to be greater than one year; therefore, phosphorus from sewage effluent will be a major nutrient source for the reservoir. High algal chlorophyll productivity will probably be maintained as TP was the most important parameter regulating Chl*a* levels. Zooplankton densities in Aquilla Lake were higher when compared to other Texas reservoirs. We expect zooplankton abundance to decline as planktivorous fish populations become established and reduction in newly-flooded organic material occurs. Because Chl*a* was moderately correlated with zooplankton, anticipated elevated levels of planktonic algae will contribute to zooplankton production. Spatial heterogeneity in the profundal benthos was possibly attributable to substrate differences, and not to water quality or reservoir level increases.

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POLLEN ANALYSIS OF LATE-HOLOCENE SEDIMENTS FROM A CENTRAL TEXAS BOG

RICHARD G. HOLLOWAY, L. MARK RAAB, AND ROBERT STUCKENRATH

Palynology Laboratory, Anthropology Department, Texas A&M University, College Station Texas, 77843, Anthropology Department, California State University, Northridge California, 91330, and Radiocarbon Laboratory, University of Pittsburgh, Pittsburgh, Pennsylvania

ABSTRACT.—Pollen analysis of a short sedimentary column from Weakly Bog, Leon Co., Texas, has provided important new evidence concerning the late-Holocene vegetational changes of central Texas. Utilization of pollen influx values have provided evidence for a shift from oak-woodland to savannah-like plant communities between 1500 and 2000 years ago, which is interpreted as the establishment of the present Post Oak Savannah. Documentation of this shift in vegetation is correlated with existing models of gradually increasing aridity and drying that have been proposed elsewhere for eastern Texas and the southern plains. *Key words:* pollen analysis; vegetational changes; late-Holocene; Texas.

Today, the region of east-central Texas is ecologically important because it is located along the prairie-forest ecotone. It was equally important in the past because it stood between the forests of eastern Texas and the dry scrub plant communities of west-central Texas. As early as the 1940's, Potzger and Tharp (1943, 1947, 1954) reported the recovery of fossil pollen from late-glacial and Holocene sediments from *Sphagnum*-bog localities in Lee, Robertson, and Milam counties, Texas. This pioneering pollen work was followed by the pollen analysis of Sofje Bog, located in Gonzales County, Texas, by Graham and Heimsch (1960) and their re-examination of some sediments from Gause Bog that had been examined previously by Potzger and Tharp (1954). This re-examination was an attempt to verify the reported occurrence of boreal conifers in late-glacial Texas sediments from this region as originally reported by Potzger and Tharp (1943).

Larson et al. (1972) reported on the pollen analysis of Hershop Bog, also located in Gonzales County, Texas. That deposit provided an almost continuous pollen record dating to 12,000 years B.P. and indicated a distinct vegetational change occurred about 10,000 yrs. B.P. from an oak-parkland to an oak-savannah dominated assemblage. Unfortunately, the most recent 2000 years of sediment were missing from this record. According to Larson et al. (1972) the bog suface vegetation had been destroyed by an attempt to drain the bog, and concomitant lowering of the water table may have destroyed the pollen assemblage for this crucial, most recent time period (Holloway, 1981).

This same phenomenon was encountered by Bryant (1977) in his examination of the pollent record from Boriack Bog, Lee Co., Texas. Again, due to draining and later over-grazing of the bog area (Bryant and

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Holloway, 1985), the upper 2000 years of the pollen record were not reported in the pollen assemblage from this core. The pollen records from earlier periods are good, yet no well-documented pollen assemblages representing the last 2000 to 2500 years of deposition are extant from this region of Texas. The pollen record from Weakly Bog, Leon Co., Texas, thus is significant because it helps close the gap in our knowledge of the paleoenvironmental history of this area by providing new information on this crucial time period in the vegetational history of central Texas during the past 2400 years.

Earlier pollen analytical studies generally reported palynological data in the form of percentage frequencies. Recently, with the advent of more precise dating methods, a better quantitative method for reporting data has become available. This method, which involves calculation of pollen influx values, was initially developed by Benninghoff (1962) and later refined by Davis (1969). Although initially designed to deal with lacustrine sediments, this method has been utilized in analyzing bog sediments. The present study is important inasmuch as it represents the first time that this statistical method has been utilized on bog sediments from Texas and allows an improved interpretation of the paleovegetational changes that have occurred within the state.

Methods and Materials

Based on evidence provided by the Espey Huston and Associates Company, Weakly Bog was located in northern Leon County, Texas, approximately five miles northwest of Jewitt. The bog area is narrow and extends over a distance of one and a half miles in an area presently delimited by the Post Oak Savannah vegetational zone (Gould, 1975). The peat deposits were relatively shallow but in some areas extended to 1.5 meters. The area is underlain by deposits of the Carrizos Sands aquifer.

A continuous column of sediment 139 centimeters in length was obtained from this deposit with a modified Livingston Piston Sampler. The core segments were extruded in the field and transferred to the Palynology Laboratory at Texas A&M University in three-inch PVC tubing. The samples were stored at 3°C until subsampled. The core sections were initially measured and described, and then split lengthwise. A subsample of one cubic centimeter was removed at 10 centimeter intervals throughout the core as well as at sedimentary contacts. Two tablets, each containing 12,330 ± 210 *Eucalyptus* pollen grains, were added to each cubic centimeter subsample following Davis (1969) for later calculation of pollen concentration and pollen influx values. The subsamples then were stored at 3°C until the fossil pollen grains were chemically extracted.

Pollen was extracted following the procedure of Faegri and Iversen (1975). Samples initially were heated for one hour in a 10 percent solution of NaOH in order to soften the organic material and remove humates. A 10 percent solution of HC1 was used inorder to remove carbonates and the samples then were screened through 200 μm mesh screen to remove the larger particles. Siliates were removed overnight by a solution of 70 percent HF. The remaining silicates and other inorganic materials were removed by a heavy density separation using $ZnCl_2$ (S.G. 1.99-2.00). Extraneous organic matter was removed by acetolysis, after which the samples were dehydrated and transferred to 1000 cs silicon oil with Butanol. For ease in identification, safranin stain was added during dehydration.

The polliniferous residue was examined using 400× magnification and minimum pollen counts of 200 grains were used throughout (Barkley, 1934). The entire slide was scanned using transect intervals of one millimeter in order to avoid the problem of nonrandom distribution of palynomorphs on the microscope slide (Brooks and Thomas, 1967). Critical identification of some grains was accomplished with 1000× magnification (oil) or Hoffman modulation phase contrast microscopy. Fungal spores and spores of cryptogamic plants were tabulated but not included within the pollen sum. Indeterminate grains, which were those too badly degraded to identify, were included within the pollen sum.

Pollen concentration (PC) values were calculated by the following formula:

$$\text{PC} = \frac{\text{number contaminant added (number fossil grains counted)}}{\text{number contaminant grains counted (sediment volume)}}$$

expressed in grains per cubic centimeter. This figure then was divided by the average rate of sedimentation as determined from the radiocarbon dates (Table 1), which produced the pollen influx values (Davis, 1969). Because of the observed sedimentary discontinuity (Table 1) at 58 centimeters, pollen influx values were calculated as two discrete units. The upper unit (58 centimeters) was deposited in 1550 years, whereas the lower unit (71 centimeters) took only 250 years for deposition.

RESULTS

Bog Stratigraphy

The basal portion of the core was composed of light-colored, fine-grained sands affiliated with the Carrizos Sands formation, common in this region of Texas. Little organic matter was present in the lower deposits (129-139 centimeters) quite unlike the situation reported elsewhere in East Texas bogs (Bryant, 1977). Due to the low organic content in the basal section of the core, the bottom section could not be radiocarbon dated, nor was pollen extracted in statistically valid quantities. All radiocarbon analyses were performed by the Smithsonian Institution Radiocarbon Laboratory and the results are presented in Table 1.

The upper 50 centimeters of the core were composed of a high fibrous, organic deposit with increasing silicate content with depth. Between 50 and 93 centimeters, the column was composed of a high silicate organic deposit with less fibrous material than in the above section, possibly the result of decomposition. This section was interrupted by two district levels. The first (50-58 centimeters) was composed of high silicates with small sand inclusions. The second level (72-76 centimeters) was a small fibrous lens. From 93 to 129 centimeters, the column was composed of silicates with an increasing coarseness and percentage of sands and silts (Fig. 1).

Pollen Results

The relative pollen frequencies clearly are dominated by *Quercus*, Apiaceae (Umbel family), and Poaceae pollen and secondarily by pollen of Cyperaceae (Fig. 1). Pollen frequency and pollen influx values, calculated by SAS (SAS, Institute Inc., 1982), can be obtained by contacting the senior author. *Pinus* pollen, while consistently present, is represented only

TABLE 1. Radiation dates from Weakly Bog, Leon County, Texas.

Smithsonian sample number	Depth	Radiocarbon years B.P.
SI-5860	20-30 cm	modern
SI-5861	50-58 cm	1550 ± 55
SI-6152	58-65 cm	2125 ± 65
SI-5861	80-90 cm	2260 ± 60
SI-6044	120-129 cm	2375 ± 65
SI-5862	129-139 cm	no date

intermittently in excess of two percent. The presence and abundance of Apiaceae pollen (four to 19 percent) is somewhat surprising, however, and probably reflects localized conditions.

The one segment of the core that does suggest some degree of variation is between 50 and 80 centimeters and is pronounced at the 75-centimeter level. As noted in the sedimentary column (Fig. 1), the 75-centimeter level was marked by a mat layer of grasses, which is interesting in that both Poaceae and Cyperaceae pollen decrease at this level. An abrupt decrease in the pollen of Apiaceae also is noted. Several taxa appear to increase at this level but not as abruptly. Pollen of *Pinus, Betula*, and *Celtis*, increase slightly and there is an apparent increase in the number of taxa at this level.

The lower portion of the core (61-124 centimeters) is characterized by extremely high pollen influx values (Fig. 2). While the pollen influx in this lower portion is dominated by *Quercus* pollen, all taxa increase in influx values. Arboreal pollen peaks between 75 and 104 centimeters. Figure

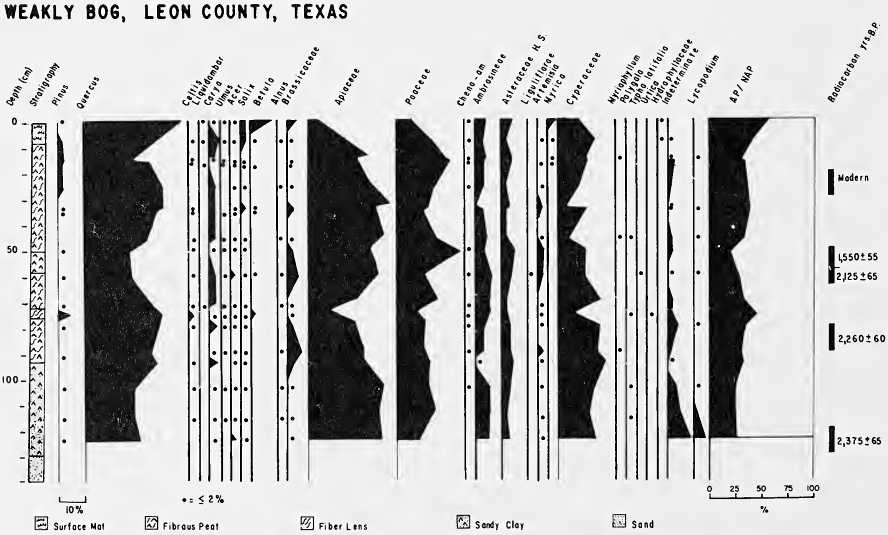

FIGURE 1. Relative pollen frequencies from Weakly Bog, Leon County, Texas.

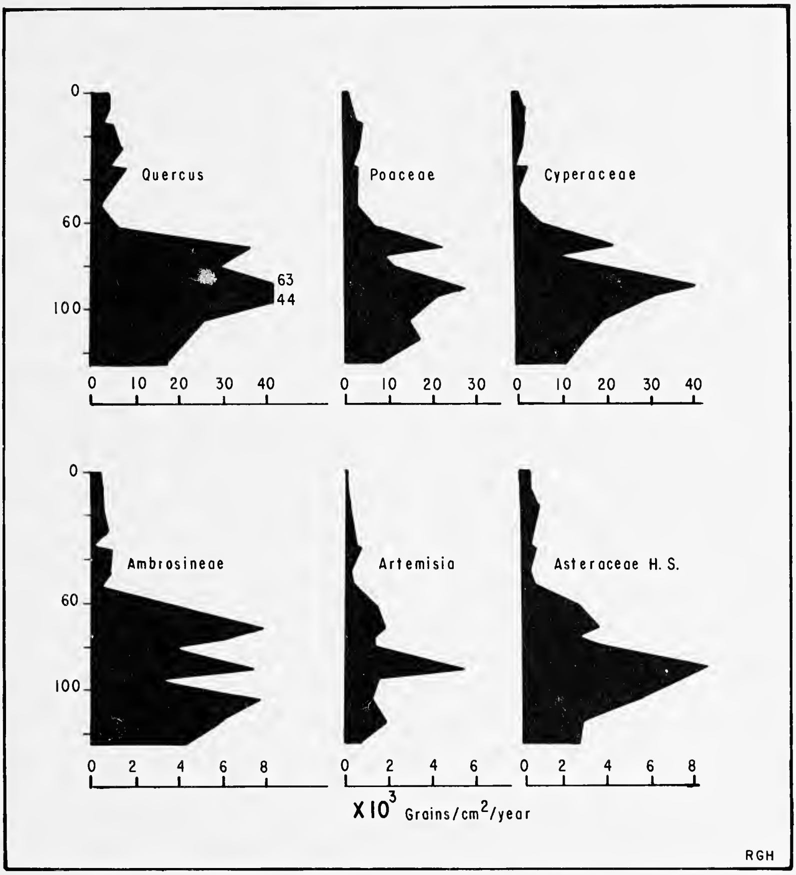

FIGURE 2. Pollen influx values of selected taxa from Weakly Bog, Leon County, Texas.

2 presents pollen influx values for selected taxa and shows that Cyperaceae, Ambrosineae, high spine Asteraceae, Poaceae, and *Pinus* pollen all decrease in the lower 20 centimeters of the core, peaking between 74 and 104 centimeters. Indeterminate pollen (Fig. 2) shows a steady increase toward the base as expected.

Pollen influx values decrease dramatically from 52 centimeters to the surface. In part, this is correlated with the mathematical manipulations of the data based on radiocarbon analysis, but the event noted is thought to be significant. Pollen influx values for all taxa are decreased and this may represent more stable conditions in this area for the past 1500 years.

DISCUSSION

Results obtained from pollen analysis of sediments from Weakly Bog show two distinct pollen assemblages, which can be interpreted as representing two major plant communities. The lower section (58-129 centimeters) shows high pollen influx values for all taxa. As indicated by the radiocarbon dates (Table 1), this section was deposited rapidly. Thus the high influx values in conjunction with rapid sedimentation agrue strongly for a dominant woodland plant community that was much denser than at present. This woodland was clearly dominated by *Quercus*, which accounts for 25 percent or more (Fig. 1) of the pollen rain and clearly shows its dominant role in the community. *Pinus* pollen is present in the assemblages yet only in minute quantities. As Davis (1969) has previously explained, when *Quercus* and *Pinus* are both present in the vegetation, *Quercus* pollen is overshadowed by the much more prolific pollen production of *Pinus*. Thus because of the low frequency of *Pinus*, even though this taxon is present in the pollen assemblage, it is interpreted as having been absent from the local community.

Alternatively, the change in sedimentation may be a function of compaction. If the lower portion of the core was compacted, this would explain the high pollen influx values. As Table 2 shows, there is no significant change in pollen concentration values throughout the length of the column as would be expected with compaction. The fact that a significant change in pollen influx values does occur at the sedimentary contact reinforces the interpretation of a shift in the distribution of the plant taxa. Because of the short time span involved with the deposition of these sediments, and the lack of concomitant changes in pollen concentration values, we conclude that no direct evidence of compaction is present. Thus it is apparent that a dramatic change in pollen influx values and sedimentation rates occurred approximately mid-way through this deposit.

Pollen influx values for nonarboreal, herbaceous taxa, especially Poaceae, in these levels (Fig. 2) are quite high. This is indicative of open areas clearly dominated by grasses and composites and is entirely consistent with the interpretation of an oak-hickory woodland.

Based on the radiocarbon data (Table 1), there is a 500 to 600 radiocarbon year erosional break occurring at the 55-centimeter level in this core. Radiocarbon dates (Table 1) suggest a 500 to 600 radiocarbon year hiatus in the sedimentation. It is only during the past 1500 years however, that pollen influx values and sedimentation rates both have decreased dramatically. The dominant taxa of the upper assemblages are not appreciably different (Fig. 1) from the earlier period, yet an abrupt change in the structure of the community does appear to have occurred. The decrease in pollen influx values may signify an expansion of hervaceous understory components and a more open, less arboreal structure to the paleovegetational community (Fig. 2). More grassland areas were present in the vicinity of Weakly Bog and, although composed of the same taxa,, the woodland was more open, resembling more a savannah. We interpret this as representing the establishment of the Post Oak Savannah in this

TABLE 2. Pollen concentration values, Weakly Bog, Leon County, Texas.

Depth (cm)	Pollen concentration	Total pollen influx
1	292,680	10,198
8	434,762	15,288
15	444,023	15,471
16	565,713	19,711
26	672,419	23,429
34	427,954	14,911
35	798,408	27,819
46	495,422	17,262
51	334,581	11,658
61	351,258	62,501
71	778,509	138,525
75	648,894	115,462
80	579,263	103,072
90	725,678	251,971
94	473,208	164,308
104	400,609	139,100
114	332,194	115,345
124	242,966	84,363
134	4,749	1,649
139	2,258	784

region of Texas. This interpretation implies a somewhat drier climate than was present earlier. Herbaceous components generally produce less pollen per plant; thus, with the decrease of arboreal taxa that would have occurred during the thinning of the forest, the pollen influx was significantly reduced. An indication of this is seen in the pollen frequency diagram (Fig. 1), which shows only slight decreases in *Quercus* pollen and concomitant increases in herbaceous pollen, although generally there is little or no change in pollen frequencies throughout the column.

The upper 25 centimeters of the core were dated as being essentially modern in age. The presence of taxa such as *Ostrya/Carpinus*, Moraceae, Anacardiaceae, *Myrica*, and *Myriophyllum* in this section suggest current conditions.

According to the radiocarbon analysis, the shift from mesic conditions to drier conditions as reflected in the decreased pollen influx values occurred at some point between 1500 and 2100 years B.P. Hall (1982), based on pollen and molluscan faunal data, recognized a gradual shift from wetter to drier conditions from a series of archaeological sites in Oklahoma. He postulated that this shift occurred about 1000 B.P., which is somewhat earlier than the date for this phenomenon suggested by Wendland and Bryson (1974) in their proposed climatic model.

Pollen analytical studies from Ferndale Bog in southeastern Oklahoma have likewise indicated a decrease in pollen concentration values somewhat later than 1554 ± 70 years B.P. (Albert, 1981). Unfortunately, these data did not include pollen influx calculations and thus cannot be compared directly with the results from Weakly Bog.

Analyses of a sediment column from Wood County, Texas (Holloway, unpublished data), is also in agreement with the record from Weakly Bog. Although preservation there was not as good as that from Weakly Bog, indications of a lowered water table and concurrent drying, which began approximately 1500 years B.P., were recognized.

On the basis of the available comparative data, the vegetational record from Weakly Bog agrees with Hall's (1982) interpretation of a gradual shift to drier conditions during the late Holocene. This shift occurred approximately 500 years earlier in central Texas than in northern Oklahoma, but supports the model of a gradual warming trend toward more xeric conditions as reported elsewhere (Bryant, 1977; Bryant and Shafer, 1977; Hall, 1982; Bryant and Holloway, 1985).

Conclusions

Pollen analysis of 139-centimeter section bog deposit recovered from Leon County, Texas, reveals a history of vegetational succession during the last 2400 years. During the earlier part of this record, the regional vegetation was composed of an oak-hickory woodland association, dominated by *Quercus* but with large prairie openings. Pine was not a member of the local plant community. Sometime between 2100 and 1500 years B.P. there was a shift to increasing aridity with the resultant reduction in arboreal cover. The canopy level was reduced yet the composition of the plant community remained virtually unchanged. Grassland areas increased in dominance with the corresponding decrease in pollen influx values.

The fossil pollen record from Weakly Bog is extremely important in that it provides new data on recent alterations to plant community structure in this region of eastern Texas. The utilization of pollen influx values, heretofore not a common practice in this region, is shown to be indispensible in recognizing these vegetational shifts.

Acknowledgements

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HABITAT AND POPULATION DESTRUCTION AND RECOVERY IN THE PARTHENOGENETIC WHIPTAIL LIZARD, *CNEMIDOPHORUS LAREDOENSIS* (SAURIA: TEIIDAE), IN SOUTHERN TEXAS

James M. Walker
Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701

Abstract.—Between June 1983 and June 1986, several local populations of the parthenogenetic whiptail lizard, *Cnemidophorus laredoensis*, were studied at sites situated between 1.6 and 2.2 km. S Chacon Arroyo, Laredo, Webb Co., Texas. During the investigation, three of the sites were subjected to catastrophic alteration by human intervention; the vegetational structure and most of the lizards at each site were destroyed by earth-grading operations. Habitat restructuring began within a few weeks, and within 14 months each of the altered sites had developed a new assemblage of grasses and weeds growing in sandy to gravelly soil. At one intensively studied site, *C. laredoensis* exhibited a rapid population recovery within a year, with more lizards being observed in the new open-structured, grass-weed assemblage than the original modified thorn shrub vegetation. As each individual is capable of reproduction in *C. laredoensis*, parthenogenesis confers an advantage over the bisexual *C. gularis* in the rapid recovery of depressed population levels as conditions return to normal in catastrophically altered habitats, or in the maintenance of low population levels under suboptimal conditions. *Key words*: whiptail lizards; Sauria; Teiidae; *Cnemidophorus*; habitat destruction and recovery.

The parthenogenetic whiptail lizard, *Cnemidophorus laredoensis*, was described from two localities in southern Laredo, Webb Co., Texas, by McKinney et al. (1973). Observations on the catastrophic destruction and recovery of the habitat and whiptail population at one of these sites, and at two others nearby, have provided some significant insights into the ecological relationships between *C. laredoensis* and one of its apparent bisexual progenitors, *C. gularis*, and into an understanding of the ecological significance of parthenogenesis in the genus *Cnemidophorus*. Data presented by McKinney et al. (1973), Bickham et al. (1976), and Wright et al. (1983) indicate that *C. laredoensis* (Fig. 1) is diploid, and originated through hybridization between *C. gularis* and *C. sexlineatus*.

Desription of Study Sites Prior to Catastrophic Alteration

I first visited the site of origin of a part of the type series of *C. laredoensis* on the east side of U.S. Highway 83 at 1.6 km. S Chacon Arroyo (designated W-3), Laredo, in July 1983. The species also was located on the west side of U.S. 83 (designated W-4), directly across from W-3, and on the east side of U.S. 83 at 2.2 km. S Chacon Arroyo (designated W-5*), Laredo, in July 1983. No individuals of *C. gularis* were observed or collected at W-3 and W-4 from 1983 through 1986; both *C. laredoensis* and *C. gularis*

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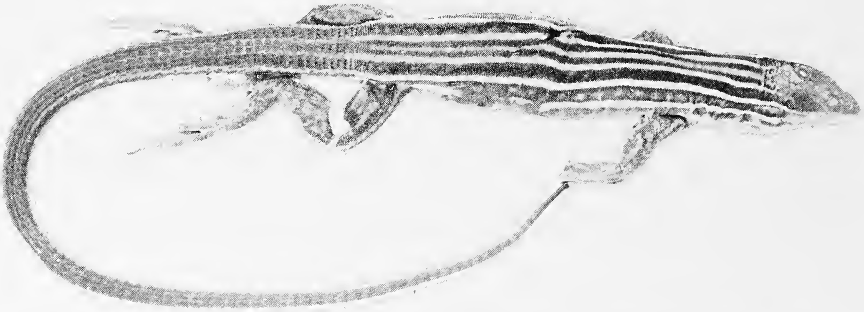

FIGURE 1. Dorsal view of an adult female of *Cnemidophorus laredoensis* from W-3 at 1.6 km. S Chacon Arroyo, Laredo, Webb Co., Texas.

were present at W-5* in 1983 and 1984. All known localities for *C. laredoensis* (sensu McKinney et al., 1973) are listed by Walker (1987); localities for the species are also cited by McCrystal et al. (1985), Dryden (1985), and Walker et al. (1986).

In July 1983, W-3 consisted of a relatively isolated, degraded patch of modified thorn shrub habitat on both sides of unpaved Saltillo Street in the southern suburbs of Laredo. The dominant vegetational components at W-3 included buffelgrass, an introduced Indo-African species (Gould, 1975), scattered clumps of *Opuntia*, and a variety of shrubs (for example, mesquite, huisache, paloverde) growing in sandy to gravelly soil. The entire area was littered with dumped debris. The south-facing side of Saltillo Street, with sand deposits to a depth of half a meter, scattered clumps of buffelgrass, and scattered debris (Fig. 2), was one of several focal microhabitats of lizard activity. Numerous burrows were present along both sides of the street and many were occupied by individuals of *C. laredoensis*.

When first observed in July 1983, W-4 consisted of a large flat area that had been extensively disrupted in the construction of a large pipeline and scraped clean of vegetation. Several *C. laredoensis* were observed along the southeastern margin in patches of buffelgrass and in buffelgrass-mesquite along the northwestern margin. Closely spaced loads of dumped waste earth rendered the southwestern part of the flat unsuitable for whiptails. Between July 1983 and July 1984, W-5* remained available as a nearby site where *C. laredoensis* and *C. gularis* could be observed or collected in syntopy. W-5* consisted of a grass-weed association of about three hectares separated from an extensive thorn shrub tract of about 25 hectares by a sandy roadbed. Most individuals of *C. laredoensis* were observed in the transition zone of the roadbed and thorn shrub vegetation, whereas *C. gularis* usually was found at the edge of, or within, the thorn shrub. Large amounts of debris were scattered between the road and surrounding habitat at W-5*.

FIGURE 2. View of habitat at W-3 looking east on unpaved Saltillo Street, 1.6 km. S Chacon Arroyo, Laredo, Webb Co., Texas, as it appeared when first visited in July 1983.

DESCRIPTION OF STUDY SITES AFTER CATASTROPHIC ALTERATION

A visit to W-3 in June 1984 revealed that the entire site had been bulldozed (Fig. 3). The thorn shrub association (dominated by mesquite) had been completely destroyed and the natural and man-made debris pushed into large mounds. The developing plant growth, dating to May 1984 according to a resident of the area, was limited to recently germinated grasses and weeds, rooting cactus pads, and root sprouts from damaged shrubs. Presumably, the scattered individuals of *C. laredoensis* that remained at W-3 were those that escaped the devastation by fleeing or by residing along the margins of the tract, rather than animals that immigrated from surrounding sites. Although both sides of Saltillo Street had been extensively disrupted from grading operations, several active burrows were located, and lizards removed from two. By July 1984, less than three months after the site was cleared, W-3 supported a low-growing grass-weed assemblage with numerous open spaces. Two additional adults of *C. laredoensis* were removed from burrows in July 1984 to confirm that whiptails were still present at W-3; however, it seemed apparent that the habitat and lizard population had been irreparably damaged. Quite the opposite proved to be the case. By the next visit to the site in July

FIGURE 3. View of habitat at W-3 looking east on unpaved Saltillo Street, 1.6 km. S Chacon Arroyo, Laredo, Webb Co., Texas, as it appeared in July 1984 about two months after earth-grading operations catastrophically altered the area.

1985, or about 14 months after the destruction of the habitat, a rapidly developing growth of grasses and weeds measuring half a meter or less in height was present (Fig. 4). Both sides of Saltillo Street had numerous burrows, from which a number of *C. laredoensis* were removed. Not only were individuals of *C. laredoensis* more widely distributed through the weedy growth in areas where they had been limited to certain microhabitats within and around the margins of the thorn shrub tract in 1983, but the number of lizards observed at W-3 indicated that an explosive recovery had occurred since the catastrophic alteration of the site. Whereas only about 30 lizards were observed by three persons in two days in July 1983, more than 50 *C. laredoensis* were observed at W-3 by four persons in only two hours in July 1985.

Although W-4 and W-5* were located in the same general area of southern Laredo as W-3, each site produced different combinations of pioneering weedy growth following their alteration. The part of W-4 that had been scraped clean of vegetation in July 1983 was found to have stands of tall sunflower, a common weed in well-drained waste areas with compacted soil in the Rio Grande Valley, when inspected in June and July 1985. Also, much of the northern third of the flat was no longer suitable for whiptails owing to its recent use as a dumpsite for waste soil. Where lizards had been limited to patches of bunchgrasses along the margins of the flat in July 1983, they were now more generally distributed through the tall sunflowers.

FIGURE 4. View of habitat at W-3 looking east on unpaved Saltillo Street, 1.6 km. S Chacon Arroyo, Laredo, Webb Co., Texas, as it appeared in July 1985 about 14 months after catastrophic alteration.

The most surprising development during the study period involved W-5*; a site inspection in July 1985 revealed that the entire 25-hectare thorn shrub tract located south and west of the sandy roadbed had been destroyed by earth-grading operations. W-5*, which had been last observed in July 1984, had become a vast and nearly impenetrable expanse of Russian thistle. Observations were mostly confined to the transition zone between the road and surrounding habitat in July 1985; *C. laredoensis* was still present at W-5*, but *C. gularis* was neither observed nor collected at W-5* in July 1985.

DISCUSSION

At the beginning of the investigation of *C. laredoensis* in 1983, the species had been reported from only two sites located 1.6 kilometers apart in Laredo, Texas, and had not been reported in México. The species is now known to occur within a narrow zone on both sides of the Rio Grande over a distance of about 250 kilometers by road in parts of Webb, Zapata, Starr, and Hidalgo counties, Texas, and the Mexican state of Tamaulipas, and well away from the river in parts of Dimmit, LaSalle, and Starr counties (Walker, 1987). Observations on sites W-3, W-4, and W-5* in Laredo, as well as on numerous other sites in the Rio Grande Valley and peripheral areas, have revealed that the local distribution of *C. laredoensis* is closely tied to the production and maintenance of disturbed areas with grass-weed associations, bunchgrass-mesquite disclimax communities, or ecotones near thorn shrub tracts from the activities of man or nature. Significantly, the three catastrophically altered Laredo sites, which differed somewhat in soil characteristics, drainage, topography, and exposure, produced three of the four plant assemblages with which *C. laredoensis* is most often associated throughout its range. A four-year study revealed that *C. laredoensis* is syntopic with *C. gularis* at a minimum of 19 of 25 localities in Texas and six of 11 in Tamaulipas. Instances of syntopy between the two taxa usually involved transtional areas between tracts of relatively undisturbed thorn shrub or remnants of such formations and grass-weed habitats or in bunchgrass/weed-mesquite formations. A common feature at all sites inhabited by *C. laredoensis* is the presence of sandy or loamy soil. *C. gularis* is adaptable to all types of soil (for example, sandy, loamy, gravelly, or rocky substrates). Whereas *C. gularis* occurs in weedy habitats with almost the same frequency as *C. laredoensis* particularly where disturbed areas abut climax formations, the natural habitat of the species includes Chihuahuan thorn shrub, barretal, and upland thorn shrub climax formations that border or intrude into the Rio Grande entrenchment. *C. gularis* may occur in small numbers or temporarily disappear from local sites that have been subjected to recent catastrophic alteration or fragmentation into small patches.

Although several authors have noted that parthenogenetic species of *Cnemidophorus* frequently are associated with ecotonal or altered habitats (Axtell, 1966; Wright and Lowe, 1968; Christiansen, 1971; Christiansen et al., 1971; Schall, 1976, 1978; Cuellar, 1977, 1979; Walker, 1987), the biological basis for this apparent pattern of ecological and geographical distribution has not been explained. Moreover, no actual observations on habitat and population destruction and recovery for a parthenogenetic form have been reported. This study indicates that the types of grass-weed habitats frequently occupied by *C. laredoensis* may begin development shortly after such catastrophic events as cultivation, earth-grading, and fire, and that an optimal habitat may develop in less than a year (Figs. 2-4). Land use patterns along the Rio Grande, which may preserve such grass-weed associations for many years or lead to the development of bunchgrass/weed-mesquite disclimax communities, often result in sufficient habitat stability for *C. gularis* to become established or remain in syntopy with *C. laredoensis*. The observations on W-3, and other similar areas in the Rio Grande Valley, indicate that parthenogenesis is at greatest advantage in *C. laredoensis* in the aftermath of habitat changes that sharply reduce the size of a population. As each individual is an effective reproductive "deme," *C. laredoensis* would be expected to persist in low numbers under suboptimal conditions more successfully than *C. gularis* because of its inherently higher reproductive rate and the lack of a requirement for a threshold population size to maintain the mating structure.

Neonates of *C. laredoensis*, which are 100 percent females, appear in July and August and grow rapidly to a snout-vent length of 55 to 60 mm before becoming inactive for the year in late November or early December. Egg production in females hatched in July and August commences the following April, and one or two clutches of two to four eggs are deposited by each female between mid-May and mid-July. With every individual in the population capable of producing eggs it is not surprising that the survivors of *C. laredoensis* at W-3 were able to generate a rapid population recovery following catastrophic alteration of the habitat. Field data from 36 sites inhabited by *C. laredoensis* indicate that the parthenogen reaches the highest population densities at sites where *C. gularis* is absent or occurs in small numbers. Whether this pattern results from interactions between lizard populations or that the same habitat conditions favoring *C. laredoensis* are inhibitory on *C. gularis* requires additional study; however, preliminary data indicate that the latter point is more important. Although *C. gularis* was present about 200 meters east of W-3 and was common at W-5* (about 0.6 kilometers south of W-3), the species has not appeared in samples from W-3 for at least 15 years (McKinney et al., 1973; C. O. McKinney, personal communication; data from this study). W-3 is locally separated from thorn shrub climax formations, the natural habitat of *C. gularis*, by streets, buildings and grounds, paved and unpaved parking lots, and expanses of grasses-weeds that impede immigration of lizards to the site. Additional conditions that may contribute to the absence of *C. gularis* at W-3 are: history of severe habitat disturbances (motor vehicles, dumping, human and animal degradation); evidence of periodic catastrophic alteration; and patchy structure of the habitat.

In summary, the parthenogen *C. laredoensis* is revealed as a pioneering vertebrate in several types of grass-weed successional stages and bunchgrass/weed-mesquite disclimax communities that today mainly result from the activities of man. The species exhibits an impressive ability to rebound from depressed population levels as a result of a parthenogenetic mode of reproduction, a biological attribute that also allows the Laredo whiptail to persist at low population levels in severely degraded habitats, and in some areas overgrown with grasses or weeds or both. The absence of the species in most areas removed from the ecological influence of the Rio Grande, and its presence in a narrow riparian zone on both sides of the river, result from its inability to become established in areas devoid of sandy burrowing sites and perhaps to the pervasive presence of *C. gularis* in climax formations.

The success of *C. laredoensis* in becoming widely distributed in communities, towns, and cities on both sides of the Rio Grande between Laredo-Nuevo Laredo and Progreso Lakes-Nuevo Progreso (that is, in areas subject to frequent habitat changes) mitigates against the species being considered endangered or threatened.

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LONG-TERM RESPONSE OF LIVE OAK THICKETS TO PRESCRIBED BURNING

Marlin D. Springer, Timothy E. Fulbright, and
Samuel L. Beasom

12508 Rosemont NE, Albuquerque, New Mexico 87112, College of Agriculture and Home Economics, Texas A&I University, Kingsville, Texas 78363 and Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville, Texas 78363

Abstract.—A 10-year prescribed burning study was initiated in 1974 on the Aransas National Wildlife Refuge, Aransas Co., Texas, to test the hypothesis that fire will reclaim grassland that has been invaded by live oak (*Quercus virginiana* Mill.). Three 700-hectare areas were burned in autumn 1974, spring 1975, and autumn 1975, with reburns at two-year intervals. Effects of repeated burns on live oak density, height, and acorn production in live oak thickets were determined. Burning increased species diversity in the forb community and favored fair to excellent forage grasses. Initial burns increased density of live oak stems by approximately 130 to 240 percent and repeated burns over the subsequent 10-year period had no further effect. Prescribed burns reduced height of live oak stems by 30 to 60 percent for up to three years. Live oak mottes generally did not burn during the first burns, but were more susceptible to subsequent burns. Burning of large trees in live oak mottes resulted in an increase in live oak stems of nearly 200 percent, *Key words*: brush management; community succession; fire; *Quercus virginiana.*

Live oak (*Quercus virginiana* Mill.) savannah, with scattered individual trees or mottes, occupies about 500,000 hectares of the Texas Coastal Prairie (Smith and Rechenthin, 1964). Historically much of the region was maintained in that condition by repeated burns of natural or aboriginal causes (Blakey, 1947; Stewart, 1963; Vallentine, 1980). In addition to occurring in mottes or as individual trees, live oak also may occur in a low, running form referred to as "running" or "shinnery" live oak (Scifres, 1980). In recent history, overgrazing and lack of fire have been implicated as contributing factors in the closing of savannahs by dense stands of shinnery live oak (Blakey, 1947; Dyksterhuis, 1957). Dyksterhuis (1957) referred to this phenomenon as the "thicketization" of savannahs.

Much effort has gone into finding ways to reverse the increasing density of oak stems and return the Coastal Prairie to savannah. Root plowing, mowing, and roller chopping have been used but are expensive (Aransas Wildlife Refuge records, 1941-74). Herbicides are effective (Scifres and Haas, 1974; Meyer and Bovey, 1980) but damage large oaks as well as shinnery. Large trees and mottes provide shade for livestock and habitat for wildlife (Scifres, 1980). Treatments used to remove low brush should leave them intact.

Because fire has influenced the development and maintenance of grasslands (including savannahs), a prescribed burning program was

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initiated to burn live oak thickets on the Aransas National Wildlife Refuge, Aransas Co., Texas, in 1974. Early effects of prescribed burning on small mammals (Brown, 1977), white-tailed deer (*Odocoileus virginianus* Rafinesque) (Springer, 1977), and vegetation (Springer, 1978; Scifres and Kelley, 1979; Kelley, 1980) were reported two years postburn. Original study plots have been burned at approximately two-year intervals since the initial burns of 1974-75. This study provided an evaluation of the long-term effects of prescribed burning on the vegetation.

MATERIALS AND METHODS

The Aransas National Wildlife Refuge is a 21,862-hectare peninsula predominated by live oak thickets. It is a part of the Coastal Prairies and Marshes Region of Texas (Gould, 1975) and is situated primarily in Aransas County. The ecology and history of the area were described by Halloran and Howard (1965) and Jones (1975).

An area of approximately 700 hectares was burned in autumn 1974 with reburns in autumn 1976, 1978, 1980, and 1983. A second area of equal size was burned in autumn 1975 with reburns in 1977, 1979, and 1981. A third area was burned in spring 1975. An unburned reference area that was sampled as a control in the first years of the study (1974-76) was inadvertently burned in 1978 and was reburned in 1980 and 1982. All sampling in burned areas was done along one, 183-meter line in each area. Lines were permanently marked with metal posts in 1974. A new unburned area of live oak thickets was chosen in 1984 and permanently marked for future reference.

For assessment of the effect of multiple burns on live oak thickets, composition of the herbaceous stratum and density, height, and acorn production of live oak were estimated on burned and unburned areas in August 1984. For comparison, some data from 1975-76 are presented.

Herbaceous composition in live oak thickets was estimated by frequency of occurrence with the step-point method (Evans and Merton, 1957). The nearest plant to a notch in the observer's boot was recorded with each step along the permanent sampling line. Data from 100 points were recorded in each area.

Density of live oak stems in live oak thickets was estimated by counting all stems in 71 plots that were 0.25 meter square and equidistantly spaced along the sampling lines. Average height of live oak was calculated from measurements of the four live stems nearest the corners of the 71 sample plots on each transect. Acorn production was estimated in live oak thickets on burned and unburned areas by counting acorns on all plants in the 71 sample plots in each area.

To assess the impact of the burning program on mottes, the woody community of five burned mottes was sampled and compared to the woody community of five unburned mottes. Five plots one meter square were equidistantly spaced along a sample line bisecting each motte. Height and density of woody plants were recorded.

The study was designed for descriptive purposes. Data were not subjected to statistical analyses because of the lack of replication and use of systematic sampling. Inferences about the results are restricted to the study area.

RESULTS AND DISCUSSION

Species Composition in Live Oak Thickets

Herbaceous communities of the burned areas in 1984 tended to be more diverse than unburned areas (Table 1); this was also true in 1975-76 (Scifres and Kelley, 1979). There were 16 species of grasses and forbs recorded

TABLE 1. Species composition (percent occurrence) of the herbaceous plant community in live oak thickets of a live oak savannah, Aransas National Wildlife Refuge, Aransas Co., Texas, August 1984. Plants identified along the sample line but not recorded as a hit were recorded as trace (t).

Species	Unburned	First burned autumn 1975[a]
GRASSES		
Seacoast bluestem [*Schizachyrium scoparium* var. *littoralis* (Nash) Gould]	20	27
Gulfdune paspalum (*Paspalum monostachyum* Vasey)	14	t
Purple lovegrass [*Eragrostis spectabilis* (Pursh) Steud.]	11	t
Switchgrass (*Panicum virgatum* L.)	8	3
Brownseed paspalum (*Paspalum plicatulum* Michx.)	5	8
Dicanthelium sp.[b]	3	11
Carpetgrass (*Axonopus affinis* Chase.)	3	t
Thin paspalum (*Paspalum setaceum* Michx.)	2	10
Big bluestem (*Andropogon gerardii* Vitman)	1	7
Bushy bluestem [*Andropogon glomeratus* (Walt.) B.S.P.]	t	6
Panicum sp.[c]	t	0
Carolina jointtail [*Coelorachis cylindrica* (Michx.) Nash]	0	t
Tumble lovegrass (*Eragrostis sessilispica* Buckl.)	0	t
Muhlenbergia sp.	0	t
Unknown grass	3	3
SEDGES AND RUSHES	20	18
FORBS		
Spadeleaf [*Centella asiatica* (L.) Urban]	6	0
Sawtooth frogfruit (*Phyla incisa* Small.)	1	t
Verbena sp.	1	t
Unknown forb	1	1
Wild bean [*Strophostyles leiosperma* (T. & G.) Piper]	0	1
Partridge pea (*Cassia fasiculata* Michx.)	0	1
Scarlet pea (*Indigofera miniata* Ort.)	0	1
Yankeeweed (*Eupatorium compositifolium* Walt.)	0	1
Snoutbean [*Rhynchosia americana* (Mill.) Metz.]	0	t
Loosestrife (*Lythrum lanceolatum* Ell.)	0	t
Dayflower (*Commelina erecta* L.)	0	t
Wild indigo (*Baptisia leucophaea* Nutt.)	0	t

[a] Burned in 1975, 1977, 1979, and 1981.

[b] Includes *D. augustifolium* (Ell.) Gould, *D. lanuginosum* (Ell.) Gould, *D. oligosanthes* (Schult.) Gould, and *D. sphaerocarpon* (Ell.) Gould.

[c] Includes *P. brachyanthum* Steud. and *P. hians* Ell.

on the unburned area in August 1984 as compared to 25 on the burned area.

In 1975-76 certain species increased, including seacoast bluestem (*Schizachyrium scoparium* var. *littoralis*) after burning (Kelley, 1980). The percent occurrence of seacoast bluestem after four burns (1984) suggested that burning may favor this species as well as big bluestem (*Andropogon gerardii*), brownseed paspalum (*Paspalum plicatulum*), bushy bluestem (*A.*

glomeratus), thin paspalum (*P. setaceum*), and some species of *Dichanthelium* (Table 1).

A difference in forb composition between the burned and unburned areas was evident in 1984. There were 11 species of forbs recorded along the sampling line in the burned area as compared to four in the unburned area (Table 1). Five of the species in the burned area were legumes that were absent in the unburned community. A more diverse legume-dominated forb community caused by burning also was indicated in 1975-76 (Scifres and Kelley, 1979).

Live Oak Density in Thickets

Two burned areas received four and five burns, respectively, over the approximately 10-year period, and density of live oak stems remained higher than preburn densities (Table 2). In 1975, live oak density in thickets of the area first burned in autumn 1974 and the area first burned in spring 1975 (one growing season postburn) had increased 150 and 240 percent, respectively, over preburn densities (Kelley, 1980). By the second growing season (1976) live oak mean density appeared to be declining on both areas, and stem density on the area first burned in autumn 1975 in its first year postburn was approximately 130 percent greater than preburn density. During this second growing season, many live oak plants (regrowth) on burned areas showed signs of severe stress. It was hypothesized that the repeated stress of burning and increased competition of the more vigorous herbaceous community would eventually reduce the number of live oak stems in burned thickets. Data taken in August 1984, however, failed to support that hypothesis. Of the two burned areas monitored in 1984, the area first burned in autumn 1975, in the third growing season since its last burn, reflected the same pattern seen in earlier years. Live oak density was about 80 percent higher than preburn levels, but 25 percent lower than the first year postburn level of 1976. Density in the area first burned in autumn 1974, in the first year postburn, was almost 300 percent greater than prior to burning. There was no change in live oak density in the unburned area in the first three years of the study.

Live Oak Stem Height in Thickets

Top kill of live oak by burning live oak thickets initially reduced stem height to ground level. Stem height of live oak regrowth remained less than stem height on the unburned area even after three growing seasons (Table 3).

Stem growth rate was greatest in the first year postburn, with progressively lower rates in the second and third years. At the rate of growth suggested by interpretation of data in the third year postburn, it was projected that it would require at least eight years for live oak in the burned thickets to reach a height approximately equal to unburned areas.

TABLE 2. Mean density (stems per square meter) of living live oak in live oak thickets of a live oak savannah, Aransas National Wildlife Refuge, Aransas Co., Texas. Numbers in parentheses indicate number of growing seasons since the last burn. Values for 1974, 1975, 1976 are adapted from Scifres and Kelley (1979) and Kelley (1980).

	Sample date			
Date of first burn	1974 (preburn)	1975 (after first burn)	1976 (after first burn)	1984 (after multiple burns)
Unburned[a]	10.0	12.8	8.0	—
A-74[b]	6.8	17.0 (1)	15.4 (2)	26.2 (1)
S-75[c]	11.2	37.7 (1)	30.9 (2)	—
A-75[d]	27.6	—	62.7 (1)	49.4 (3)

[a] Unburned reference area was inadvertently burned in 1978.
[b] Burned in the autumn of 1974, 1976, 1978, 1980, and 1983.
[c] Burned in the spring of 1975.
[d] Burned in the autumn of 1975, 1977, 1979, and 1981.

Acorn Production in Live Oak Thickets

Although top-killed live oak is capable of flowering and producing acorns on regrowth stems the first year postburn, it appeared that most energy was used in vegetative regrowth. In 1984, one growing season after the last of five burns, acorn production on live oak regrowth was less than acorn production on live oak in unburned thickets (Table 4). Burning-related reduction in acorn production was significant both as production per unit area and production per plant. Production of acorns per unit area on burned thickets in their second and third year postburn tended to be lower than on unburned areas. When compared as production per plant, production was lower on burned areas. This same trend was evident in 1975-76 (Springer, 1978).

TABLE 3. Mean heights (cm) of living live oak stems in live oak thickets of a live oak savannah, Aransas National Wildlife Refuge, Aransas Co., Texas. Numbers in parentheses indicate number of growing seasons since the last burn. Values for 1975 and 1976 are adapted from Scifres and Kelley (1979) and Kelley (1980).

	Sample date		
Date of first burn	1975 (after first burn)	1976 (after first burn)	1984 (after multiple burns)
Unburned	48.8	53.6	42.7
A-74[a]	23.4 (1)	28.8 (2)	15.6 (1)
A-75[b]	—	16.4 (1)	29.1 (3)
A-78[c]	—	—	24.1 (2)

[a] Burned in the autumn of 1974, 1976, 1978, 1980, and 1983.
[b] Burned in the autumn of 1975, 1977, 1979, and 1981.
[c] Burned in the autumn of 1978, 1980, and 1982.

TABLE 4. Mean production of acorns in live oak thickets of a live oak savannah, Aransas National Wildlife Refuge, Aransas Co., Texas, August 1984.

Treatment	Acorns per square meter	Acorns per stem
Unburned	32.2	1.7
Burned areas[a]		
First growing season postburn (after five burns)	0.3	0.01
Second growing seasons postburn (after three burns)	17.0	0.3
Third growing seasons postburn (after four burns)	15.6	0.3

[a] All burned areas have had 3-5 burns over a 10-year period.

Woody Composition of Mottes

Although large mottes generally did not burn in the initial burns of 1974-75, observation in later years indicated that with each successive burn, mottes became more susceptible to burning. A comparison of aerial photography from 1974 and 1984 showed that approximately 20 percent of the area occupied by the original mottes had burned.

After mottes burned, there was an increase in the number of live oak stems (throughout the original area encompassed by the motte) (Table 5). Shade tolerant species, typical of the understory of unburned mottes, remained in approximately the same densities on burned mottes.

CONCLUSIONS

Prescribed burning over a 10-year period, with burns at approximately two-year intervals, was not effective in reducing live oak density in thickets in live oak savannah on the Aransas National Wildlife Refuge. Although fire is widely accepted as one of the main factors in the formation and maintenance of grasslands, results of this study indicate that fire cannot be used to restore grasslands on the Refuge. It is effective in reducing height of live oak and probably in increasing availability of the area for wildlife and livestock. This effect, coupled with a more diverse postburn herbaceous community, suggests that the prescribed burning program can

TABLE 5. Mean density (stems per square meter) of major woody species (live plants) in the mottes of a live oak savannah, Aransas National Wildlife Refuge, Aransas Co., Texas, August 1984.

Species	Unburned	Burned
Live oak (*Quercus virginiana* Mill.)	0.9	2.6
Yaupon (*Ilex vomitoria* Ait.)	1.2	1.0
Beautyberry (*Callicarpa americana* L.)	0.4	0.4
Catbriar (*Similax bona-nox* L.)	0.6	1.2
Mustang grape (*Vitis mustangensis* Buckl.)	0.3	0.1

have practical benefits if burns are repeated at intervals frequent enough to maintain suppression of live oak height.

Burning of mottes removed the large tree canopy cover and promoted formation of thickets. It may be desirable to preserve mottes because of their value as shade for livestock and habitat for wildlife. Fire lines could be constructed around the mottes to protect them from burning.

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NOTEWORTHY RECORDS OF MAMMALS FROM THE TEXAS PANHANDLE

ROBERT R. HOLLANDER, J. KNOX JONES, JR., RICHARD W. MANNING, AND CLYDE JONES

Departments of Biological Sciences and Museum Science, and The Museum, Texas Tech University, Lubbock, Texas 79409

ABSTRACT.—Distributional and natural history data are presented for 12 species of mammals—one shrew, three bats, the armadillo, and seven rodents—from the Texas Panhandle. *Key words*: distribution; mammals; Panhandle, Texas.

The Panhandle area of northern Texas is one of the least well known in the state from a zoological point of view, perhaps because of its sometimes inhospitable climate and relative lack of species diversity, and because it is far removed from most centers of biological study. All but the eastern edge of the Panhandle lies in the High Plains physiographic region. Some of the salient environmental features of the High Plains and the Rolling Plains adjacent to the east were described by Gould (1975). Environmental variables of the region were summarized by Owen and Schmidly (1986).

In 1984, we began a survey of mammals in the Panhandle, concentrating our efforts primarily in the northern counties—those areas lying to the north of the Canadian River. Specimens thus far accumulated, along with some material already housed in The Museum of Texas Tech University (TTU), represent 12 species that are noteworthy in terms of distribution, taxonomy, and natural history. These data are recorded here.

Notiosorex crawfordi crawfordi (Coues, 1877)

The only previous report of the desert shrew from the northern part of the Texas Panhandle is of a specimen taken in the flood plain of Bugbee Creek, 9 mi. E Stinnett, Hutchinson County (Blair, 1954:241). We have at hand a nonpregnant female (TTU 6849) taken 14 mi. E and 7 mi. S Dumas, Moore County, on 27 June 1968 by W. H. Conley.

Lasiurus borealis borealis (Müller, 1776)

The only published record of the red bat from the Panhandle of which we are aware is the specimen reported by Blair (1954:242) from 9 mi. E Stinnett, Hutchinson County. We took a lactating female (TTU 42648) on the Tyson Ranch, 8 mi. NW Higgins, Lipscomb County, on 26 July 1985. It was the only bat captured in a mist net set over a spring in a small, open canyon.

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Plecotus townsendii pallescens (Miller, 1897)

This big-eared bat, which probably occurs in suitable places throughout the Panhandle, has been reported previously only from Armstrong County (Davis 1974:69). We have examined a female (TTU 2038) that was obtained in Borger, Hutchinson County, on 11 May 1965, and three specimens from Collingsworth County—two males (TTU 43684-85) taken in hibernation in a large gypsum sinkhole, 4 mi. N and 13 mi. E Lutie, on 8 March 1986, and a female (TTU 43686) netted over Elm Creek, 3 mi. N and 12 mi. E Lutie on 13 May 1986. The female carried a single fetus (23 mm in crown-rump length).

Antrozous pallidus pallidus (Le Conte, 1856)

The pallid bat is known from the Panhandle on the basis of a specimen from Tascosa, Oldham County (Bailey, 1905:214), and small series from Briscoe and Deaf Smith counties (Martin and Schmidly, 1982:31-32). In the summer of 1985, we netted a series of adult *A. pallidus* (TTU 42650-92), all but one males, in the steep canyon of Romero Creek on the Griffin Ranch, 17-18 mi. N and 1 mi. E Adrian, Oldham County, and another series (TTU 42693-725) on the Fain Ranch, 16 mi. N Amarillo, Potter County, which included adults and young-of-the-year of both sexes. These were taken along with *Eptesicus fuscus* at the entrance to a barn used as a night roost. Additionally, on 13 May 1986, a female (TTU 43687), pregnant with twins (crown-rump lengths 17 and 19 mm), was taken in a mist net set over Elm Creek, 3 mi. N and 12 mi. E Lutie, Collingsworth County. *Myotis velifer, Pipistrellus subflavus, Plecotus townsendii* (see above), and *Tadarida brasiliensis* were netted at the same place.

Dasypus novemcinctus mexicanus Peters, 1864

The armadillo is recorded from the Panhandle only from Armstrong County (Davis, 1974:269). We found one (TTU 42726) of unknown sex dead on U.S. Highway 60 at a place 10 mi. SW Canadian, Hemphill County, an extension of known range of approximately 80 miles to the northeast. Additionally, it was reported to one of us (Hollander) by a reliable observer that one had been killed 7 mi. NW Higgins, Lipscomb County, on State Highway 213, on about 4 July 1985. Probably the armadillo occurs throughout at least the eastern part of the Panhandle region.

Sciurus niger rufiventer É. Geoffroy St.-Hilaire, 1803

Fox squirrels have been reported previously from Hemphill and Hutchinson counties in the northern part of the Panhandle but the distribution there is not well documented. We have two additional records from the north side of the Canadian River in Hemphill County—3 mi. E. Canadian (TTU 42731) and 13 mi. E Canadian (TTU 42730).

Additionally, the collection at Texas Tech University contains six specimens from Hansford County, three from 3 mi. S and 6 mi. W Gruver (TTU 270-72) and three from 10 mi. S and 3 mi. W Gruver (TTU 269, 273-74).

In the summer of 1985, Hollander observed several fox squirrels in cottonwoods along Pitcher Creek, a tributary of the Canadian River, 16 mi. N Amarillo, Potter County, and at least two others at Boys Ranch, on the north bank of the Canadian in Oldham County. This squirrel undoubtedly occurs in suitable habitat all across the Panhandle along the Canadian and its immediate tributaries, and also in the drainage basin of the North Canadian or Beaver River in the extreme northeastern part.

Geomys bursarius jugossicularis Hopper, 1940

This subspecies has been recorded from one locality in the northwestern part of the Panhandle—15 mi. E Texline, Dallam County (Hall and Kelson, 1952:364). Tentatively, we assign specimens from 1 mi. N and 3 mi. W Dalhart, Dallam County (TTU 42749-50), and 1 mi. S Dalhart, in Hartley County (TTU 42751-56), to *G. b. jugossicularis* because they are noticeably paler than pocket gophers collected to the east of those localities (Collingsworth, Hemphill, Lipscomb, and Moore counties) that represent *G. b. major.*

In a study of pocket gophers of the genus *Geomys* in Texas, Davis (1940) did not examine material from the northwestern Panhandle and, in fact, did not map *Geomys* as occurring in that area. Similarly, Honeycutt and Schmidly (1979) did not treat gophers from that part of the Panhandle, possibly because of the paucity of specimens then available. Hart (1978) recognized *G. b. jugossicularis*, placing it in his "*bursarius* group" of subspecies, whereas Heaney and Timm (1983) regarded *jugossicularis* as a synonym of *lutescens*, which they reckoned as a species distinct from *bursarius*. Whatever the ultimate fate taxonomically of pocket gophers from the northwestern Panhandle, they do appear to represent a paler race than specimens from farther to the east and south.

Castor canadensis Kuhl, 1820

Both Davis (1974:190) and Schmidly (1984:5) mapped the beaver as occurring only in the extreme eastern part of the Panhandle. We observed indisputable evidence of this rodent (complete with photographs) near the mouth of Romero Creek, on the north side of the Canadian River, 17 mi. N and 1 mi. W Adrian, Oldham County. Furthermore, local residents informed us that beavers inhabited Pitcher Creek, on the Canadian 16 mi. N Amarillo, Potter County, within the past five years, and this species also was reported to us as resident below the dam of Lake Meredith in Hutchinson County. Evidently, *C. canadensis* occurs sporadically along the Canadian and its major tributaries. The subspecific identity of the Panhandle population is questionable.

Reithrodontomys megalotis aztecus J. A. Allen, 1893

The western harvest mouse is generally uncommon in the Panhandle and evidently only locally distributed there. We are aware of only three previously reported specimens—one from Hutchinson County and two from Hansford County (Jones and Mursaloğlu, 1961:21). We have collected 22 specimens to date, all taken in grassy-weedy habitats with good ground cover, from the following localities: 4 mi. N and 1 mi. E Dumas (TTU 43050-51), and 3 mi. S Dumas (TTU 43052), Moore County; 10 mi. N Stratford (TTU 43899-901), and 8 mi. S and 2 mi. E Stratford (TTU 43902-17), Sherman County. The percentage of tail length to length of head and body in our mice is less than typical for *R. m. aztecus* (83.7 percent in 20 adult specimens as opposed to an average of more than 90 in specimens of *aztecus* examined by Jones and Mursaloğlu, *op. cit.*), suggesting the need for detailed systematic study of this species in the Panhandle and adjacent areas.

Baiomys taylori taylori (Thomas, 1887)

Two adult pygmy mice, one of each sex, were trapped along a grassy-weedy fencerow, adjacent to mesquite pastureland, 9 mi. E Lutie, Collingsworth County, on 14 May 1986. These not only provide the first records of this rodent from the Panhandle, but represent the northernmost point of known occurrence in North America. Furthermore, the locality of capture lies but a few miles west of the Oklahoma line, a state whence *B. taylori* is known from a single specimen recently reported from just north of the Red River in Cotton County (Stangl and Dalquest, 1986:123).

The male (TTU 43780) had testes measuring 3 × 2 mm; the female (TTU 43779) carried three fetuses that were 5 mm in crown-rump length.

Neotoma albigula warreni Merriam 1908

Davis (1974:220) did not map the white-throated woodrat as occurring in the northern part of the Panhandle, although Cutter (1959:448-449) reported specimens from Hansford and Hutchinson counties, referring them to the subspecies *warreni* on the basis of coloration, size, and several cranial features. Subsequently, Rogers and Schmidly (1981:180) recorded specimens of *N. a. warreni* from Moore and Potter counties. We collected nine rats of this species in rocky habitats at the following localities: 5 mi. W Boys Ranch (TTU 42824-25), 6 mi. W Boys Ranch (TTU 42823), and 18 mi. N and 1 mi. W Adrian (TTU 42818-22), all in Oldham County, and 4.8 mi. NW Sanford, Hutchinson County (TTU 42817).

We have compared our material with specimens of *N. a. albigula* from several places near the type locality in Arizona and with specimens of *N.*

a. warreni from Cimmaron County, Oklahoma. They definitely agree with the former in color, but with *warreni* in cranial details as described by Rogers and Schmidly (*loc. cit.*).

Erethizon dorsatum bruneri Swenk, 1914.

The porcupine probably ranges sparingly throughout the Panhandle. The only record from north of the Canadian River, however, is of one found dead in a cottonwood grove 9 mi. E Stinnett, Hutchinson County (Blair, 1954:254), which was overlooked by Davis (1974). We found one killed on FM 767 at a locality 6.4 mi. W Channing, Hartley County, on 23 August 1985. Only the left dentary and tail (TTU 43103) of this animal could be salvaged.

We follow Hall (1981) in referring our specimen to *E. d. bruneri.* Systematics of *E. dorsatum* in Texas and adjacent regions are deserving of serious study.

Acknowledgments

We are indebted to several Texans who assisted our efforts in the field, but most especially to the John Henard family of Collingsworth County, Sam Mason of the Griffin Ranch in Oldham County, Robert Morris of the Fain Ranch in Potter County, Donald Tyson of the Tyson Ranch in Lipscomb County, officials of Cal Farley's Boys Ranch in Oldham County, and Craig S. Hood, Texas Tech University. Field work was supported in part by funds made available by the Graduate School and Office of Research Services, Texas Tech University.

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GENERAL NOTES

RANGE AND HABITAT EXPANSION OF THE INTRODUCED SLUG, *ANGUSTIPES AMEGHINI*, IN EXTREME SOUTHERN TEXAS

Raymond W. Neck
Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744

Of the veronicellid slugs that have become established in the Brownsville, Cameron Co., Texas, area (Neck, 1976, 1981, 1985), the most abundant is *Angustipes ameghini* (Gambetta, 1923). Native only to Paraguay (Gambetta, 1923), *A. ameghini* also is known from other localities on the Gulf Coastal Plain of the southern United States (Dundee, 1974; Burch and Van Devender, 1980). Initial Brownsville records were from urban residential yards (Neck, 1976). Stange (1978) reported that *A. ameghini* in Florida was "an urban slug found in vacant lots and cemeteries." The purpose of this note is to report expansion of range to an adjacent county and recent dispersal to native brush tracts within Cameron County.

Living individuals of *A. ameghini* were collected at two localities in Hidalgo County, Texas: 1) Edinburg—urban residential yard, 317 Enfield Road, slugs found under bricks and flower pots in garden area, four specimens collected on 28 September 1983, had been seen by occupants for "about three years" (Audrey and Wayne Holiman, personal communication); and 2) Santa Ana National Wildlife Refuge—landscaped area around headquarters building and nearby transplant garden-greenhouse area, five specimens collected on 13 and 14 October 1984 by Joe Ideker, seen only recently (dried bodies discovered during personal survey on 27 September 1984).

Additional localities from urban habitats other than yards in Brownsville and native brush habitats near Brownsville in Cameron County are as follows: 1) Town Resaca at Boca Chica Blvd., Brownsville, five slugs found under downed branches in second-growth brush at edge of water, 22 June 1984, five additional slugs found 200 meters north in more open area with wood on ground, 21 October 1984; 2) Esperanza Ranch-area with remnant native brush habitat along Resaca de la Palma at eastern edge of Brownsville, three slugs found under downed mesquite trunk, 22 October 1984; and 3) West Palm Grove—3.1 kilometers southeast of the Esperanza Ranch site, remnant palm-thorn scrub woodland, two slugs found underneath palm leaf litter, 22 October 1984.

These additional Cameron County records are the first valid records of *A. ameghini* that are not from residential yards. The report from Rabb Palm Grove (Neck, 1976) actually refers to *Sarasinula plebeia* Fischer, 1868, a species that has not been observed at this locality since the original collection on 23 December 1970. The significance of the Town Resaca records is the ability of *A. ameghini* to survive in feral populations without direct supplemental water, although such habitat areas along resaca shorelines are quite restricted. The occurrence of *A. ameghini* at the Esperanza Ranch site indicates that brush communities associated with resacas also may be able to support this species. The West Palm Grove locality is not associated with a resaca and is a much more xeric area than the two localities previously mentioned.

The initial Hidalgo County records and additional Cameron County records provide some insight into probable dispersal routes utilized by *A. ameghini* as well as likely limits of habitat suitability in the lower Rio Grande Valley. The Santa Ana population is apparently the result of slugs present in commercial nursery stock of local native plants that were brought onto the refuge. The Edinburg population further demonstrates that *A. ameghini* is being dispersed

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within extreme southern Texas. The Town Resaca populations were founded by overland dispersing slugs over short distances from nearby residences. The more isolated nature of the Esperanza Ranch indicates that drainage ditches and resacas carrying urban runoff water may function as dispersal routes of *A. ameghini.* Field surveys have revealed no hint of the origin of the West Palm Grove population as this area is isolated from urban drainage by the levee system that limits the floodwaters of the Rio Grande.

The environmental factor likely to be most important in limiting geographic and ecologic occurrence of *A. ameghini* in southern Texas is moisture rather than extreme winter temperatures. Populations of *A. ameghini* tend to be more restricted in Edinburg than Brownsville. Edinburg is both drier and cooler than Brownsville, although the differences are small. Feral populations in native brush communities no doubt will exhibit lower densities and suffer higher extinction rates than those in urban residential lawns. Significantly, *A. ameghini* is the most drought-tolerant of the three introduced veronicellids that have established populations in Brownsville.

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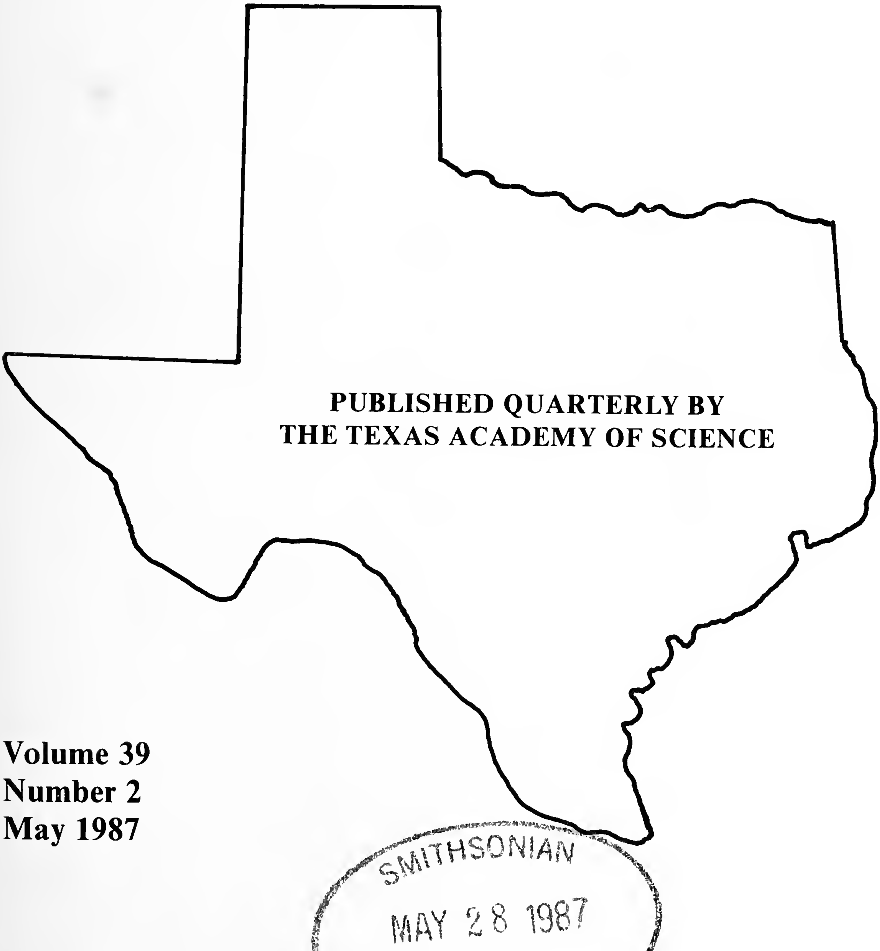

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AGGRESSIVE AND DEFENSIVE PROPENSITIES OF *SOLENOPSIS INVICTA* (HYMENOPTERA: FORMICIDAE) AND THREE INDIGENOUS ANT SPECIES IN TEXAS

Stanley R. Jones and Sherman A. Phillips, Jr.
Department of Entomology, Texas Tech University, Lubbock, Texas 79409

Abstract.—Since its accidental introduction into Mobile, Alabama, the red imported fire ant, *Solenopsis invicta* Buren, has become a pest in much of the southern United States. Each year this ant continues to expand its range. The reasons *S. invicta* is able to colonize successfully areas already inhabited by multifarious ant species are not understood; however, possible explanations include its aggressive behavior, reproductive capacity, large colony size, and foraging efficiency. This laboratory study was conducted to compare the aggressive and defensive behaviors of *S. invicta* and three native ant species of central Texas with one another. Native ants studied were *Pheidole dentata* Mayr, *Forelius foetidus* (Buckley), and *Monomorium minimum* (Buckley). We found interspecific differences in aggressive and defensive abilities. *Solenopsis invicta* and *P. dentata* were more aggressive than *F. foetidus* and *M. minimum*. Although the latter two species exhibited the least aggression, they displayed the greatest defensive abilities. *Key words: Solenopsis invicta*; aggression; defense; native ants.

The invasion and disruption of long-established populations of indigenous ant species by foreign ant species have been recorded on numerous occasions. Way (1953) reported the near total replacement of the dominant *Oecophylla longinoda* Latreille of eastern Africa by *Anoplolepis longipes* (Jerdon) introduced from India. Similarly, *Pheidole megacephala* (F.) has successfully displaced native ant species from numerous tropical and semitropical oceanic islands (Zimmerman, 1970). *Iridomyrmex humilis* Mayr also has undergone massive range expansion at the expense of other ant species (Haskins and Haskins, 1965; Fluker and Beardsley, 1970; Erickson, 1971). More recently, Clark et al. (1982) and Lubin (1984) found that *Wasmannia auropunctata* (Roger) has a negative impact on many of the ant species of the Galapagos Islands through interference competition. Finally, MacKay and MacKay (1982) stated that *Formica haemorrhoidalis* Emery can invade and completely eliminate the nests of *Camponotus laevigatus* (F. Smith) in southern California. However, unlike the previous examples cited, both of these sympatric species are native and could perhaps coexist indefinitely.

The red imported fire ant, *Solenopsis invicta* Buren, has had similar success displacing ants indigenous to the southern United States (Wilson and Brown, 1958). Reagan et al. (1972) reported that *S. invicta* is the only ant species found by extensive pitfall trapping in Louisiana sugarcane fields following invasion by this species. Whitcomb et al. (1972) also reported that the presence of *S. invicta* in the fields of northern Florida reduces the densities of the native ant fauna. Buren et al. (1974) reported the

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apparent elimination of *Solenopsis xyloni* McCook by *S. invicta* from several Louisiana pastures.

Despite the apparent success and aggressiveness of *S. invicta*, several studies have revealed that this ant may not be so successful during individual encounters with other species, or when interspecific colony sizes are equal. Bhatkar (1973) demonstrated that the defensive abilities of at least six ant species indigenous to Florida exceed those of *S. invicta*. Also, Bhatkar et al. (1972) presented evidence that a single *Lasius neoniger* Emery worker is capable of killing two to three *S. invicta* workers. The success of *S. invicta*, therefore, is most likely due to high fecundity and overwhelming numbers, rather than to individual aggressive ability.

An additional factor that may affect the ability of native ant species to successfully compete with, and coexist with, *S. invicta* is defensive ability. Several authors have alluded to this concept, but few have dealt with it specifically. Howard and Oliver (1979) stated that many ants in a Louisiana pasture tended to avoid conflict. Bhatkar (1973) stated that individuals of various ant species often demonstrate momentary defensiveness prior to escape from those of a more aggressive species. Several ant species apparently possess specialized behaviors or morphological adaptations allowing superior defensive ability. For example, *Pheidole dentata* Mayr has an enemy-specific alarm-recruitment system that alerts colony members to approaching intruders (Wilson, 1976). *Monomorium minimum* (Buckley) uses a drop of venom on its sting as an effective deterrent and irritant to would-be attackers (Baroni-Urbani and Kannowski, 1974; Adams and Traniello, 1981). A sticky fluid, discharged from the repugnatorial gland of *Forelius foetidus* (Buckley), acts as both repellent and irritant and, in some cases may be fatal to attacking ants (Wheeler, 1910).

The three myrmicine species *S. invicta*, *P. dentata*, and *M. minimum* and the dolichoderine species *F. foetidus* consistantly occurred at high frequencies during an extensive, year-long sampling study conducted by Rogers (1984) in Kerr and Bandera Counties, Texas. That study indicated that these ant species coexist in the same habitats. Given that *S. invicta* has been established in Kerr and Bandera counties for approximately 10 years, we may reasonably assume that the other three species are coexisting with, and successfully competing with *S. invicta*. Therefore, the following laboratory study was conducted to compare the aggressive and defensive abilities of these four ant species and to understand better the mechanisms involved in their apparent coexistence.

Materials and Methods

Colonies were collected from Kerr, Bandera, and Lubbock counties, Texas, during their diurnal periods of lowest foraging activity, corresponding to early morning for *F. foetidus* and *M. minimum*, and early afternoon for *P. dentata* and *S. invicta* (authors observation). Colonies of *M. minimum* and *F. foetidus* contain monomorphic workers, whereas workers of *P. dentata* are dimorphic, resulting in majors and minors. However, *S. invicta* workers are polymorphic, consisting of minors (head width 0.72 mm or less), medias (head width 0.73-0.92 mm), and majors (head width 0.93 mm or more) (Wilson, 1978).

Aggression.—Propensity for aggression or combative ability was ascertained by placing a predetermined number of ants of different species in plastic containers (11 by 11 by 4 centimeters). The bottom surface of each container was lined with moist Castone dental plaster, providing a rough substratum as well as a moisture reservoir to prevent ant desiccation. One milliliter of distilled water was added to the containers prior to each test. The sides of each container were coated with Fluon to prevent ant escape. Each test was conducted at 30°C under fluorescent lighting and 70 to 75 percent relative humidity. Ten individuals of one species-caste were simultaneously placed in a container with 10 individuals of another species-caste. Castes of *S. invicta* as defined by Wilson (1978) were determined by measuring head capsule widths. Individuals were then left undisturbed for three hours, after which the number alive and dead were recorded. Individuals that retained movements but were incapacitated, were recorded as dead. Ten individuals of each species-caste were maintained in separate containers and served as controls. These procedures resulted in 17 confrontation pair groups, each of which was replicated eight times. Data were analyzed with two-tailed Student t-tests, first for each species group, then for each caste within species, thus yielding a comparative indication of combative ability for each species and each species-caste.

Defensiveness.—Propensity for defensiveness or avoidance of confrontation was tested by placing a single individual of one species-caste with that of another. Containers for these trials consisted of petri dishes (60 by 20 millimeters) coated on the sides with Fluon. Temperature and humidity conditions were as above. Again, the 17 species-caste combinations were made, each with 15 replications.

Following placement of two individuals into a container, the number of contacts made between each was recorded every 60 seconds for a maximum of 10 minutes. If a contact resulted in overt aggression leading to death, the time of this occurrence was recorded. Data were analyzed with a nested ANOVA followed by Student-Newman-Kuel's multiple comparison test.

RESULTS

Aggression

Species combative performances are presented in Figure 1. No significant differences were detected between the combative abilities of *P. dentata* and *S. invicta* (t = 0.35), *P. dentata* and *M. minimum* (t = 0.78), or *F. foetidus* and *M. minimum* (t = 1.93). However, *S. invicta* was significantly greater in combative ability over *F. foetidus (t* = 4.55) and *M. minimum* (t = 7.07), whereas *P. dentata* was superior in ability only to *F. foetidus* (t = 8.55).

Results of combative abilities for the 17 species-caste combinations are presented in Figure 2. The general trend during three hours of confrontation between larger species-castes of similar size (pair groups 1-6) was that, regardless of species, the larger caste of the pair group was more aggressive and had greater combative ability. This trend can be noted for *S. invicta* majors and *P. dentata* minors (t = 36.56), *S. invicta* medias and *P. dentata* majors (t = 22.54), *S. invicta* medias and *P. dentata* minors (t = 14.76), and *S. invicta* minors and *P. dentata* majors (t = 39.00). However, the combative abilities of the latter two species were the same when equal-

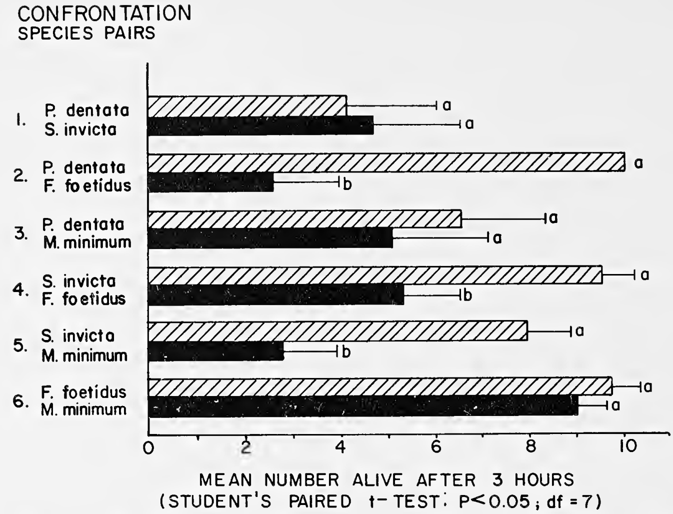

FIGURE 1. Results of two-species confrontation trials among four ant species. Data analyzed by Students' t-tests. Means with the same letter are not significantly different ($P > 0.05$) within species pair (n = 10 ants/species).

sized castes were compared (pair groups 1 and 6). No significant difference was detected between *P. dentata* and *S. invicta* majors (t = 0.42) nor between *P. dentata* and *S. invicta* minors (t =2.05).

Comparing combative ability of the larger species-castes versus the smaller species (pair groups 7-12), significant differences were detected in every instance. *Pheidole dentata* majors were greater in combative ability than those of *M. minimum* and *F. foetidus* (t = 22.29; t = 99.00), as were *S. invicta* majors (t = 19.94; t = 3.47). In addition, *S. invicta* medias were significantly greater in ability than those of *M. minimum* (t = 7.76) and *F. foetidus* (t = 3.47). However, whereas *P. dentata* majors killed all *F. foetidus* (pair group 8), the impact of *S. invicta* majors and medias on *F. foetidus* (pair groups 10 and 12) was not as great.

Comparing smaller species-castes of similar size (pair groups 13-17), no difference in aggression was detected between *S. invicta* minors and *M. minimum* minors (t = 1.36) nor between those of *M. minimum* and *F. foetidus* (t = 1.93). Although *P. dentata* minors and *S. invicta* minors were superior to *F. foetidus* minors (t = 3.98; t = 5.31), *M. minimum* minors were greater in ability than minors of *P. dentata* (t = 10.12). All ants maintained as controls during each of the 17 trials survived the three-hour trial durations.

Defensiveness

The results of trials involving defensive abilities are presented in Figure 3. Analysis of defensive abilities or avoidance of aggression indicates that

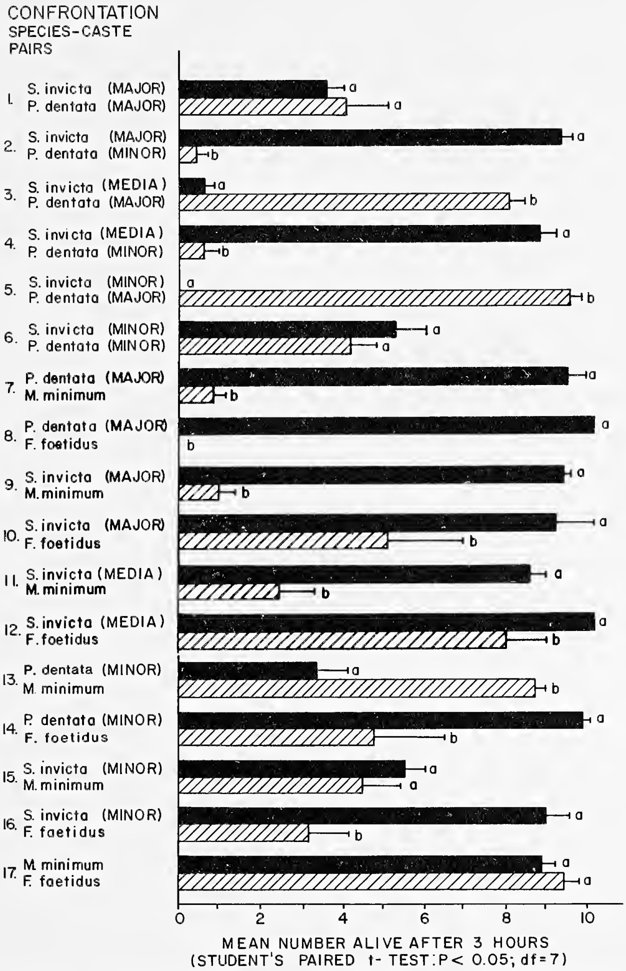

FIGURE 2. Results of confrontation trials for all 17 species-caste combinations. Data analyzed by Students' t-tests. Means with the same letter are not significantly different ($P > 0.05$) within species-caste pair (n = 10 ants/species-caste).

differences do occur in species-caste pairs (F = 24). Although the mean number of contacts of pairs 1-8 was large, no significant differences were detected among them prior to overt aggression. Seven of the pairs from that group involved *M. minimum* and *F. foetidus* paired with either *P. dentata* or *S. invicta*, whereas one pair involved *M. minimum* and *F. foetidus*. Note that, within this group, either both species-castes within a pair were small or the size discrepencies among species-castes within a pair were large, resulting in a greater number of contacts than detected in pairs 9-17. Results from this latter group indicated that, in general, as size of the species-caste increases and the size difference of the species-caste within

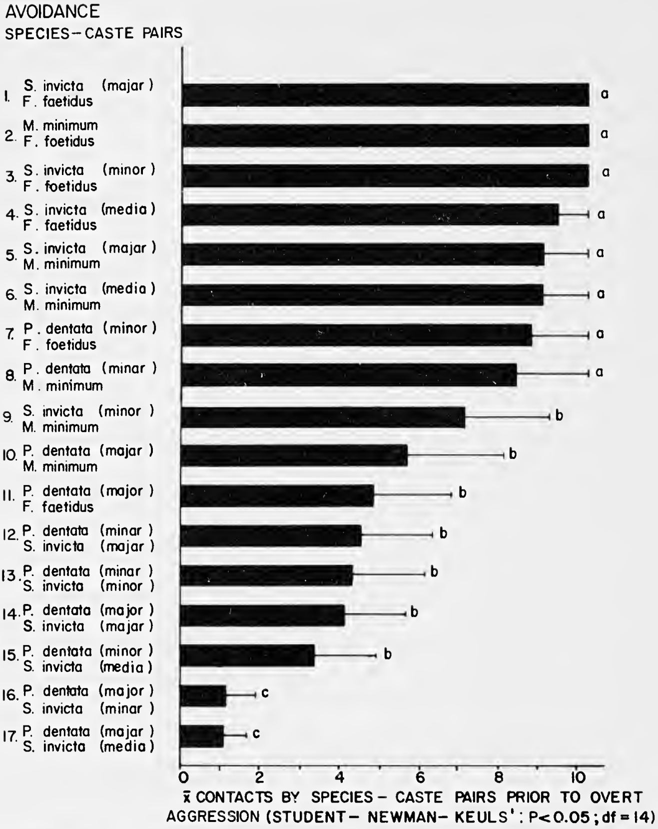

FIGURE 3. Comparison of defensive abilities within all 17 species-caste combinations. Data analyzed by Student-Newman-Kuels' test. Means with the same letter are not significantly different ($P > 0.05$) within species-caste pair (n = 10 ants/species-caste).

each pair decreases, the number of contacts prior to overt aggression also decreases. This trend was particularly evident between *P. dentata* and *S. invicta* (pairs 16 and 17).

DISCUSSION

Laboratory observations revealed that in tests of both aggression and defense, *S. invicta* and *P. dentata* were the aggressor species, whereas *F. foetidus* and *M. minimum* were more defense oriented. Though forced, prolonged interactions between these ant species-castes are not necessarily the typical interactions occurring in nature, they do provide useful insight into the methods used and success obtained during interspecific confrontations. In situations of forced, prolonged interaction, *P. dentata* and *S. invicta* were superior in terms of species combative ability. In general, smaller castes were less successful in competition with larger castes.

Individuals tended to be most aggressive toward ants slightly smaller than themselves. Ants of similar size were less aggressive toward each other, and were better able to survive aggressive encounters than were individuals of disparate sizes. *Pheidole dentata* majors were more aggressive than all other species and castes tested with the single exception of *S. invicta* majors. If aggression and defense alone are considered, one would expect *S. invicta* to have difficulty displacing colonies of *P. dentata* in nature. However, *S. invicta* colony members outnumber those of *P. dentata* several-fold. In addition, the major caste of *P. dentata* comprises a mere 20 percent of the total worker force (Wilson, 1976), thus limiting their effectiveness during large-scale encounters.

Under natural circumstances, individual foragers usually meet once, followed by immediate directional changes and separation (authors observation). Often, an ant of the more aggressive species will attempt to attack an individual of a less aggressive species, but these attempts are seldom successful. The smaller, less aggressive species such as *F. foetidus* and *M. minimum* employ a highly effective chemical interference, which deters attack and allows for escape from aggressors (Wheeler, 1910; Baroni-Urbani and Kannowski, 1974). Note that *F. foetidus* and *M. minimum* exhibited the greatest number of contacts prior to fatal combat during defensive ability trials (Fig. 3). In fact, *M. minimum* and *F. foetidus* appeared in all of the top eight trials. This finding demonstrates that during individual foraging encounters, the probability of escape or avoidance of conflict by *F. foetidus* and *M. minimum* is high, but decreases with increasing number of contacts. Because the probability of numerous encounters over short time periods is unlikely during normal foraging activity, the benefits obtained by effective chemical defense are great. The chemical repellent used by *M. minimum* and *F. foetidus* is generally referred to as defensive in nature (Baroni-Urbani and Kannowski, 1974; Adams and Traniello, 1981). However, observations of these two species in confined arenas made the distinction between defensive and offensive use of these chemicals less clear. The two species often appeared to use their chemical "defense" in an offensive manner. In communities where *S. invicta* population densities are low, *P. dentata* may compete successfully with *S. invicta* because of their highly specialized and aggressive soldier caste. Similarly, *F. foetidus* and *M. minimum* may compete successfully by avoiding direct aggression via effective chemical defense.

Potts et al. (1984) suggested that *S. invicta* colony number and population densities may be severely affected by periods of water stress. Xeric conditions may limit food availability as well as reproductive output of fire ant colonies. Francke et al. (1986) demonstrated that *S. invicta* are not freeze tolerant and that their northern limits of distribution appear to be correlated to winter temperatures. These two factors suggest that as *S. invicta* expands its range northward and westward into more xeric and gelid conditions, colony densities (mound and individual numbers within each mound) should decrease. This is, of course, barring any rapidly acquired ability of *S. invicta* to survive these adverse abiotic conditions.

As the densities of *S. invicta* decrease along the leading edge of range expansion, their numbers may more closely approximate those of the indigenous ant species, specifically *P. dentata*, *F. foetidus*, and *M. minimum*. Interspecific combative abilities then could approximate those found during this study. Because the indigenous ant species of Texas north and west of the current range of *S. invicta* are well adapted to their respective climatic conditions, their ability to effect a more significant degree of resistance on the further expansion of *S. invicta* may become apparent.

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SAMPLING EFFORT AND BIAS IN SOFT-SEDIMENT BENTHIC INVESTIGATIONS USING THE PETERSON DREDGE

Frank S. Shipley

Texas Water Commission, 400 Mann St., Suite 905, Corpus Christi, Texas 78401

Abstract.—Eight replicate Peterson grabs of uniform mud substrate were taken in central Matagorda Bay, Texas, to assess within-site variability in organism densities among replicates. Based upon Morisita indices calculated on organism counts in the replicates, 41 percent of species were significantly aggrigated; none was distributed uniformly in spite of the homogeneous substrate at the study site. Most large species, like mollusks, and some small but infrequent species were undersampled by single grabs. Cumulative number of species increased asymptotically with sampling effort, indicating a need for multiple replicates to adequately characterize species composition. However, 97.9 percent of all individuals taken belonged to species taken in the first two replicates, indicating that the numerical composition of the community could be characterized in relatively few grabs. *Key words*: sampling effort; sampling bias; Peterson dredge; benthic; Morisita index; Matagorda Bay, Texas.

Representative sampling of benthic marine organisms is difficult because many factors cause their distributions to depart from random. Species distributions may be influenced by substrate preference (Aller and Dodge, 1974), response to salinity or other water quality regimes (Rosenberg and Moller, 1979), and tolerance of disturbance (Boesch et al., 1976). Besides these physical factors, additional distributional patterns are imposed by biological interactions such as competition, predation, or coloniality (Woodin, 1974; Peterson, 1977). Finally, even randomly distributed organisms are likely to be undersampled, if they occur at low density in relation to the capacity of the sampling apparatus.

As a result of nonrandom distributions in benthic organisms, biological patterns of interest may be difficult to distinguish from sampling variability. Most investigators are interested in demonstrating community differences between benthic habitats, or perhaps temporal changes in a particular habitat, but to do so, sampling error must be factored out. For example, statistical tests like ANOVA require estimates of within-site variability in order to distinguish differences between sites. In this investigation, I attempted to characterize within-site variability in Peterson sample counts to increase confidence in between-site community characterizations for a study in the same area to be reported elsewhere.

Materials and Methods

Eight Peterson grabs, each sampling one square foot (929 square centimeters) of substrate were taken near channel marker 16, central Matagorda Bay, Texas (Fig. 1). Sediment at this open bay location is uniform soft clay, allowing complete penetration of the Peterson apparatus to procure samples of about 20 liters. The site has stable salinities of approximately

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23 parts per thousand (surface) and a water depth of three to four meters. Samples were washed through a 0.59-millimeter sieve on board the sampling vessel, and material retained by the sieve was narcotized in isotonic MgCl solution for about half an hour, preserved in buffered 10 percent formalin, and returned to the laboratory for vital staining with rose bengal, sorting, and identification. Organisms were identified to species in most cases, excepting nemertines. Variability in counts for each species among repicates was calculated as the coefficient of variation (CV), which corrects for gross differences between rare and common organisms. Morisita indices (Morisita, 1959) were calculated to test for nonrandom dispersions as a source of bias in sampling. The Morisita index is a dimensionless value for which <1 indicates ordered dispersion; exactly 1, random; and >1, clumped. The index is calculated as:

$$I\delta = \frac{\sum_{i=1}^{q} n_i (n_i - 1)}{N(N-1)},$$

where n_i equals the number of individuals in the i^{th} replicate ($i = 1,2,3...q$), q equals the number of replicates, and N equals the number of individuals in all replicates. $I\delta$ is independent of distribution type, number of replicates, and count magnitude differences, and lends itself to variance ratio testing for departure from random dispersion. Finally, cumulative number of species was plotted against sampling effort to quantify the diminishing returns associated with increasing effort. The cumulative percent of total individuals represented by these species in successive grabs was compared on this plot to assess the numerical portion of the community that could potentially be underrepresented at each sampling effort.

RESULTS AND DISCUSSION

Nonrandom dispersion of organisms could contribute to sampling variability if some replicates included aggregations of organisms and others did not. The Morisita index calculated for each species (Table 1) resulted in significantly more values ≥1, compared to <1 (23 as opposed to four; binomial probability $P < 0.01$). This result indicated a trend toward aggregation (mean species Morisita value, 1.42). Total organism counts (all species) ranged from 88 to 214 per replicate, indicating variability in overall organism densities.

Individual species varied in dispersion. For the 36 species, coefficients of variation on counts across replicates ranged from 0.23 (*Paraprionospio pinnata*) to 2.83, in four species from just a single replicate each. Eleven of the 27 species for which sufficient data existed showed a significant departure from one (random dispersion) in Morisita value (two-tailed variance ratio $P < 0.05$). In each of these species, the value was greater than one, indicating aggregation. Other species, for example the abundant polychaete, *Paraprionospio pinnata*, apparently were dispersed at random and showed good repeatability among the grab samples. There were no clear cases of ordered dispersion among the species taken, even though the substrate was apparently uniform.

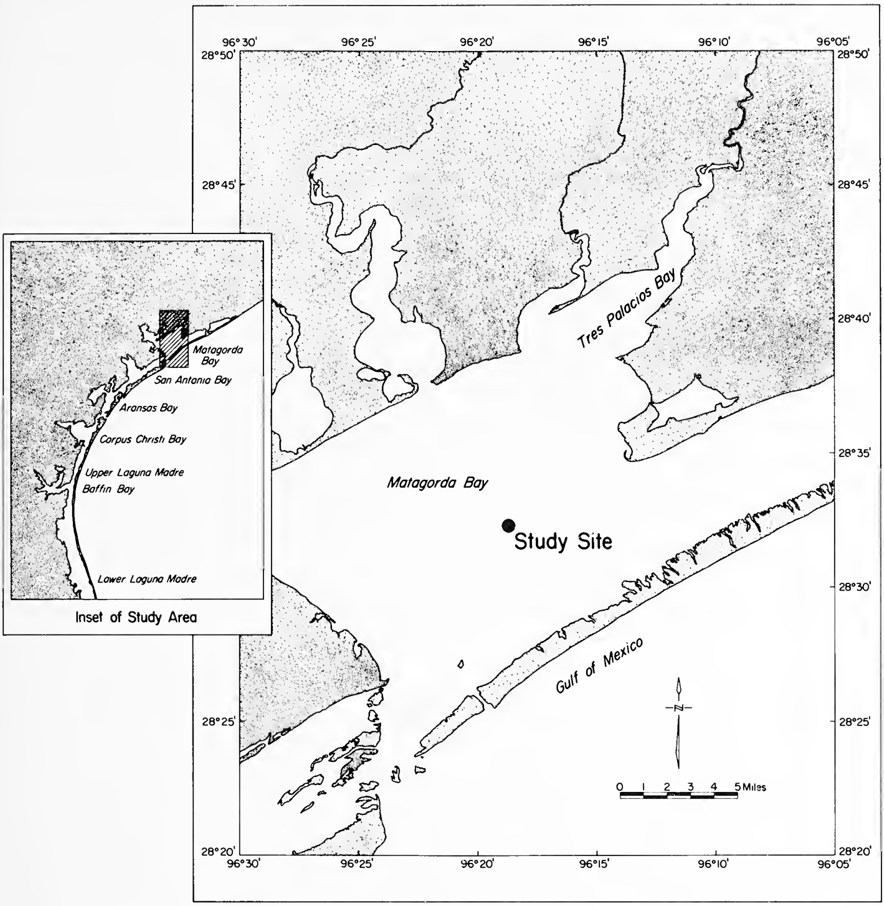

FIGURE 1. Location where samples were taken, with inset showing the location of Matagorda Bay on the Texas Coast.

For some low-density species, single grabs sampled insufficient substrate to allow reliable density estimates. Arthropods, and particularly mollusks, tended to be large-bodied and infrequent, and some polychaetes, though small, were rare enough to appear in just one or several samples. Some of these species produced high CV and Morisita values, but the small sample size preculuded statistical conclusions regarding their dispersion.

A mean of 23.5 species occurred per replicate, or 65.3 percent of the 36 species occurring in all replicates, indicating substantial undersampling of species by single grabs. In this case, taking two grabs instead of one would have (on the average) increased the number of species collected by 26 percent. The slope of the cumulative species plot decreased with sampling effort (Fig. 2, lower curve) toward an asymptote somewhere at or beyond eight replicates, at which point essentially all species would be represented.

TABLE 1. Benthic organisms obtained in replicate Peterson dredge samples of soft sediment, Matagorda Bay, Texas

	Sample Replicate									
Organisms	1	2	3	4	5	6	7	8	Mean (CV)	Morisita
Phylum Nemertina										
Sp. A	19	7	3	5	7	3	6	1	6.38(0.87)	1.53**
Sp. B	5	5	3	1	4	3	2	2	3.13(0.47)	0.91
Sp. C	2	9	2	5	2	13	6	5	8.00(0.84)	1.29*
Sp. D	3	0	1	0	0	0	0	0	0.88(1.55)	4.00*
Sp. E	0	0	1	0	0	0	1	1	0.38(1.38)	—
Phylum Mollusca										
Polinices duplicatus	0	0	0	0	1	0	0	1	0.25(1.85)	—
Nassarius vibex	0	0	0	1	1	2	2	1	0.88(0.95)	0.76
Nuculana concentrica	3	1	1	3	1	0	2	0	1.38(0.86)	1.02
Mulinia lateralis	0	0	0	1	0	0	0	1	0.25(1.85)	—
Tellina texana	1	0	0	0	2	3	0	1	0.88(1.28)	1.52
Abra aequalis	1	0	0	0	0	1	0	0	0.25(1.85)	—
Phylum Annelida										
Leitoscoloplos fragilis	3	0	4	0	1	9	2	0	2.38(1.29)	2.15**
Aricidea sp.	4	0	2	1	8	1	3	2	2.63(0.95)	1.49*
Cossura delta	12	19	16	8	20	18	20	10	15.38(0.31)	1.03
Paraprionospio pinnata	16	20	19	11	15	14	19	11	15.63(0.23)	0.99
Prionospio cirrifera	1	0	0	1	3	2	0	1	1.25(0.83)	1.14
Streblospio benedicti	0	2	0	0	0	0	0	0	0.25(2.83)	—
Magelona cf. *phyllisae*	0	0	0	0	1	0	0	1	0.25(1.85)	—
Mediomastus ambiseta	0	16	2	19	60	46	53	42	29.75(0.79)	1.51**
Maldane sp.	1	0	0	0	0	0	0	0	0.13(2.83)	—
Asychis elongatus	6	1	2	2	1	1	3	4	2.63(0.67)	1.10
Pokarkeopsis levifuscina	1	1	5	0	5	4	3	4	2.88(0.68)	1.11
Sigambra sp.	2	2	4	0	2	1	4	1	2.00(0.71)	1.00
Glycinde solitaria	9	7	3	2	5	6	10	8	6.25(0.45)	1.04
Pseudeurythoe ambigua	1	7	8	4	11	11	17	5	8.00(0.62)	1.23**
Euphrosine sp.	4	2	2	1	14	0	6	3	4.00(1.11)	1.89**
Gattyana cirrosa	0	3	0	1	2	1	0	3	1.28(1.02)	1.24
Diopatra cuprea	0	0	0	1	3	1	0	0	0.63(1.70)	2.40
Onuphis magna	1	0	0	0	0	0	0	0	0.13(2.83)	—
Lumbrineris tenuis	2	3	4	5	7	4	4	3	4.00(0.38)	0.90
Phylum Sipuncula										
Phascolion strombi	2	1	1	0	0	3	0	0	0.88(1.29)	1.52
Phylum Arthropoda										
Eudorella hispida	16	5	13	7	9	9	6	21	10.75(0.51)	1.15**
Leptognatha caeca	0	7	11	6	22	4	16	6	9.00(0.79)	1.45**
Sp. A	0	0	0	0	0	3	0	0	0.38(2.83)	—
Ogyrides limicola	0	1	0	0	5	4	3	1	1.75(1.13)	1.67*
Phylum Echinodermata										
Micropholis atra	0	1	8	3	2	3	2	5	3.00(0.84)	1.33
Total Individuals	115	120	115	88	214	170	190	144	144.50(0.30)	1.07**

*Significantly different from 1.0, $P < 0.05$.

**Significantly different from 1.0, $P < 0.01$.

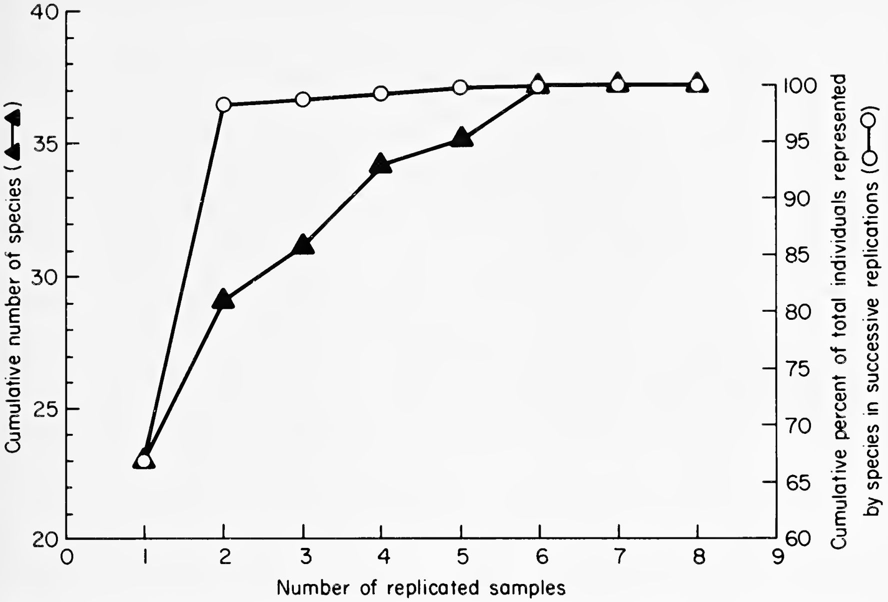

FIGURE 2. Cumulative number of species captured is plotted as a function of sampling effort (left axis). The cumulative percent of all individuals represented by the species captured in successive grabs also is shown (right axis). The axes are calibrated so the curves begin at the same point.

However, the species added with successive replications represented a strongly decreasing numerical proportion of the organisms composing the community (Fig. 2, upper curve). For example, the 29 species taken in just two replicates represented 97.9 percent of all individuals, whereas the seven additional species added in the subsequent six replicates, combined, made up the remaining 2.1 percent of all individuals. By these results, sampling efforts aimed at determining species composition of a community would require more replications than those aimed at determining patterns for numerically dominant members of the community.

Benthic sampling design involves a trade-off between effort per replicate and number of replicates. For each sampling site, the greatest information per unit effort occurs with the least replication, but for the information to be meaningful in comparing locations, multiple samples become necessary to overcome system noise. Variability in organism counts among samples in this study was influenced by the propensity for some species to aggregate in spite of apparently homogeneous substrate. For such species, within-site variability in density is high, requiring numerous replications if valid comparisons are to be made with other communities. Several species, however, showed a nearly random dispersion, allowing reliable density estimation with much less work. Finally, grab volumes were insufficient in relation to the low densities of some infrequent species, for which density estimates could not be evaluated. For these species, alternative sampling apparatus should be considered. While there is little reason to assume these results apply exactly to other substrate types, or even to other soft bottom locations, they do emphasize the need for knowledge of species dispersion patterns prior to attempting community comparisons.

ACKNOWLEDGMENTS

I thank James Bowman for help in sampling, and Bob Trebatoski and Tom Calnan for their constructive comments on the work.

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LAMPROPELTIS SIMILIS FROM THE COFFEE RANCH LOCAL FAUNA (HEMPHILLIAN LAND MAMMAL AGE) OF TEXAS

Dennis Parmley

Department of Biology, Midwestern State University, Wichita Falls, Texas 76308

Abstract.—Matrix recently collected from the Coffee Ranch local fauna of Texas (Hemphillian Land Mammal Age) has yielded a well-preserved trunk vertebra of *Lampropeltis similis.* This record is important because current knowledge of the herpetofauna of the Hemphillian Land Mammal Age is deficient. Moreover, this record extends the paleogeographic occurrance of this species approximately 350 kilometers to the south and extends its geologic range approximately three million years into the mid-Hemphillian Land Mammal Age (about 6.6 million years B.P.). *Key words*: *Lampropeltis similis*; Coffee Ranch local fauna; Hemphillian Land Mammal Age; Texas.

Matrix recently collected from the Coffee Ranch fossil site (Hemphillian Land Mammal Age), Hemphill County, Texas, has yielded a vertebra of the extinct snake *Lampropeltis similis.* Little is known about the small amphibians and reptiles of the Hemphillian of Texas (or elsewhere in North America), thus the record is of considerable interest. Traditionally, the Hemphillian Land Mammal Age was believed to belong to the middle Pliocene (Wood et al., 1941). More recently, the correlations of Berggren and Van Couvering (1974) indicated that the latest part of the Hemphillian straddles the Miocene-Pliocene boundry. Land mammal age names are used here in lieu of classical geochronologic nomenclature. The Coffee Ranch contains the type local fauna of the Hemphillian Land Mammal Age (Wood et al., 1941; Evernden et al., 1964; Dalquest, 1969), and an age of 6.6 million years B.P., based on Zircon fission tracks, is available for the hard volcanic ash that covers the quarry (Izett, 1975). Dalquest (1983) considered this to be a minimum date and believed the age of the Coffee Ranch sediments and fauna might be greater than 6.6 million years B.P. Further, based on his informal three-part division of the Hemphillian Land Mammal Age, the Coffee Ranch local fauna is considered mid-Hemphillian. The geology and mammalian fauna of the Coffee Ranch local fauna have been described in detail by Dalquest (1969, 1980, 1981, 1983) and are not discussed here. Parmley (1984) reported one salamander, turtle shell fragments (*Geochelone*), and six species of snakes (two boids and four colubrids) from the Coffee Ranch local fauna. *Lampropeltis similis*, here reported, is new to the paleoherpetofauna of the Coffee Ranch.

Species Account and Discussion

Lampropeltis similis was described by Holman (1964) on the basis of trunk vertebrae from the Valentine Formation (Barstovian) of Nebraska.

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A single trunk vertebra of *L. similis* (Midwestern State University Collection of Fossil Vertebrates 12304; Fig. 1a-d) was recovered from approximately 400 kilograms of Coffee Ranch matrix. The vertebra is nearly complete and the basis of identification used here are those discussed by Holman (1964) for the holotype vertebra (University of Nebraska 61035). The combination of characters that identify the Coffee Ranch vertebra to species follows. In dorsal view, the vertebra is somewhat square in appearance (cl/naw 1.30 mm). The right accessory process is broken, but the left process is nearly complete. It is short, rounded at the end, and positioned slightly oblique to the long axis of the centrum. The dorsal surface of the neural spine is rounded. The right side of the zygosphene is broken but this structure appears to be crenate in shape. In ventral view, the hemal keel is well developed, narrow, and relatively uniform in width along its entire length. The subcentral ridges are well developed, with deep valleys between them and the hemal keel. In lateral view, the neural spine is longer (2.7 mm) than high (1.2 mm measured from the top of the zygosphene to the top of the neural spine), has a slight posterior overhang, and the anterior edge slopes gently outward. The subcentral ridges arch slightly upwards. The hemal keel expands posteriorly (see Fig. 1c) indicating the vertebra was positioned near the cervicals. The condyle is slightly oblique (points dorsally) to the long axis of the centrum. In anterior view, the zygosphene is slightly, but noticeably, convex and relatively thin. The cotyle is oval in shape. The neural canal is dome-shaped and slightly larger than the cotyle. In posterior view, the neural arch is moderately depressed. The condyle is well developed and rounded. The Coffee Ranch vertebra agrees well with the holotype but represents a larger snake. The length through the zygapophyses is 4.7 mm (4.0 for holotype), the width through the zygapophyses is 5.5 mm (4.8 for holotype), and the height from the lower lip of the cotyle through the top of the zygosphene is 3.5 mm (3.1 for holotype).

Lampropeltis similis previously has been reported from the Barstovian through the Clarendonian of Saskatchewan (Barstovian), South Dakota (Barstovian), Nebraska (Barstovian), and Kansas (Clarendonian) by Green and Holman (1977), and Holman (1964, 1970, 1973, 1975). The occurrence of this species in the Coffee Ranch local fauna extends its known paleogeographic range approximately 350 kilometers (217 miles) south of the Kansas locality (Fig. 2), and extends its temporal chronologic range approximately three million years into the medial Hemphillian Land Mammal Age (about 6.6 million years B.P.).

The phylogenetic relationship of *Lampropeltis similis* to other species of fossil and Recent *Lampropeltis* from the United States is speculative at present. Holman (1964) postulated that *L. similis* may be ancestral to *L. intermedius* Brattstrom, from the Blancan of Arizona and Mexico, which in turn may be the stem stock for the Recent species *L. triangulum, L.*

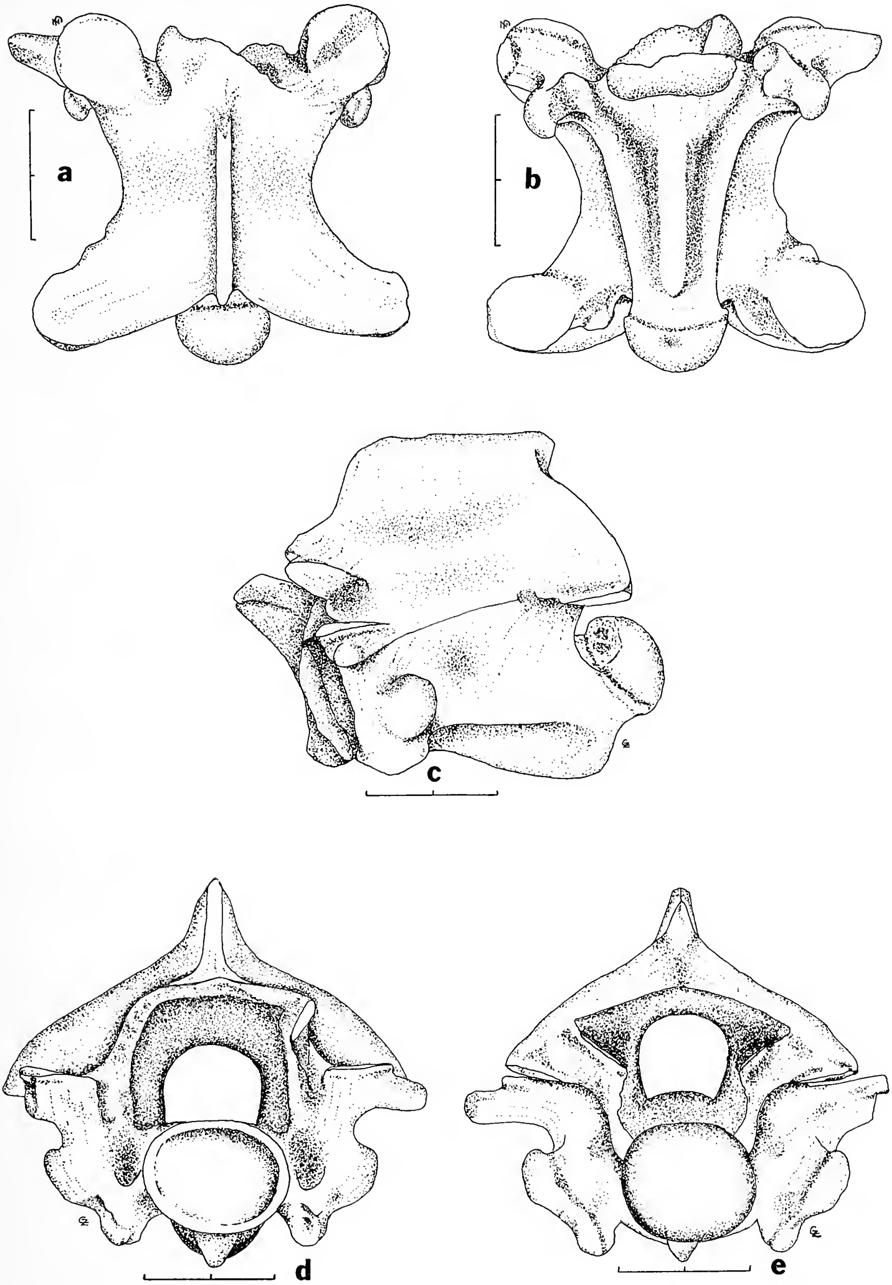

FIGURE 1. Coffee Ranch *Lampropeltis similis* vertebra in dorsal (a), ventral (b), lateral (c), anterior (d), and posterior (e) views. Line equals 1 mm.

FIGURE 2. Fossil (1-6) occurrence of *Lampropeltis similis* and Recent (boxed) range of *L. triangulum*. See text for fossil records.

zonata, and *L. pyromelana*. Brattstrom's (1955) description and illustrations of *L. intermedius* vertebrae seem somewhat subjective. He stated that *L. intermedius* differs from Recent *L. triangulum* in that the centrum ridges, when viewed from below, are narrower towards the condyle in *L. triangulum*. Numerous Recent *L. triangulum* skeletons were examined during this study and the centrum ridges appear to be individually variable. I have seen *L. triangulum* vertebrae that match perfectly Brattstrom's (1955) diagramatic views and description of *L. intermedius*. *L. similis* vertebrae indicate a rather generalized *Lampropeltis* that appears to be linked to the Recent species *L. triangulum, L. zonata, L. pyromelana*, and *L. mexicana*, in that all have small vertebrae with low, relatively long, neural spines and depressed neural arches.

How *L. getulus* and *L. calligaster* fit into this phylogeny is not clear. Both species have higher neural spines and usually more vaulted neural arches than the above-listed species. *L. getulus* and *L. calligaster*, however, sometimes have neural spines, neural arches, and subcentral ridges identical to those in *Elaphe obsoleta* and *E. guttata*, making them impossible to distinguish from one another. A close relationship between *Lampropeltis* and *Elaphe* has been reported (Bury et al., 1970; Baker et al., 1972; Garstka, 1982). Thus, based on information currently at hand, I suggest the following: 1) *L. intermedius* probably should be considered indeterminant; 2) a common ancestor gave rise to *Elaphe* and *Lampropeltis*, with *L. getulus* and *L. calligaster* representing a separate line of *Lampropeltis* evolution; 3) *L. similis* is probably the common ancestor to the Recent species *L. triangulum, L. zonata, L. pyromelana*, and *L. mexicana*; 4) *L. similis* became extinct sometime during mid-to-late-Hemphillian times.

While the ecological requirements of *Lampropeltis similis* are not known, speculations inferred from the known requirements of Recent taxa thought to be modern relatives are suggested here. Based on its large geographic range during Barstovian through mid-Hemphillian times, it must have been a snake with broad ecological tolerances. The only Recent North American *Lampropeltis* with a north-to-south geographic range approaching that of *L. similis* is *L. triangulum* (Fig. 2). It may be that *L. similis* was similar to *L. triangulum* and was a nocturnal constrictor that fed chiefly on reptiles and small mammals. Its relatively low, long neural spine is indicative of fossorial or secretive forms (Holman, 1973). *L. similis* may have been secretive, spending a great part of its time beneath rocks or logs, or burrowed into soft soils.

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AN ASSESSMENT OF GEOGRAPHIC AND SEASONAL BIASES IN SYSTEMATIC MAMMAL COLLECTIONS FROM TWO TEXAS UNIVERSITIES

Frederick B. Stangl, Jr., and Elizabeth M. Jones
Department of Biology, Midwestern State University, Wichita Falls, Texas 76308, and The Museum, Texas Tech University, Lubbock, Texas 79409

Abstract.—Geographic and seasonal biases are inherent to regional mammal collections, and are generally reflective of faculty research interests and the academic calendar of institutions housing collections. We assessed the extent of seasonal and geographic biases for 11 species of mammals, represented by museum study skins, in the collections of two Texas universities—Texas Tech University and Midwestern State University. Causes and possible solutions of such biases are discussed so that curators and collection managers may improve geographic and seasonal representation of their collections. *Key words*: systematic mammal collections; collection biases; collection management; specimen collections.

Systematic collections of mammals may include comprehensive accumulations of local species. Proximity of an institution to favored habitats of locally occurring taxa affords an opportunity to acquire series of specimens that characterize seasonally variable features of a given species. Many such features also vary geographically, and a regional collection thus becomes an important component of a network of similar collections for such studies as geographic variation, reproductive activity, molt, and growth and development.

Regional mammal collections affiliated with colleges or universities usually reflect past and present faculty and graduate student research activities (voucher specimens), student collections, financial support for collecting and curatorial efforts, and the academic calendar of the institutions. These factors insure the individual nature of different collections. The collections of Texas Tech University (TTU) and Midwestern State University (MWSU) are illustrative of this. A brief historical perspective of the two mammalogy programs and resulting collections is useful in understanding collection composition and collecting patterns of Texas mammals documented in this study.

The TTU mammalogy program was established by the late Robert L. Packard in 1962, and currently numbers seven professional mammalogists and their more than a dozen M.S. and Ph.D. students. The collection currently contains about 45,000 specimens and is rapidly expanding. Classes involving field collecting currently are offered in the autumn, and student collections consist mostly of animals taken on class field trips away from the immediate Lubbock vicinity and often out-of-state. An increasing emphasis on extra-regional representation is mostly reflective of current faculty and graduate student research interests.

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Although the MWSU collection has some important holdings from outside Texas, it is primarily regional in coverage and currently contains about 15,000 specimens. The mammalogy program was initiated in 1952 by Walter W. Dalquest, who currently is joined by the senior author. The graduate program is small, and M.S. students with interest in mammalogy are occassional. Classes involving field work traditionally have been offered in the spring. Student collecting efforts frequently are directed locally. Faculty and graduate student research interests mostly are restricted to Texas mammals. Many specimens also have been collected incidental to paleontological surveys throughout the state by Dalquest and his students.

Although biases in systematic mammal collections may be expected, we have found that seasonal and regional misrepresentation may be unexpectedly great in some instances. We realize that total alleviation of a documented imbalance may be difficult, but attempts to minimize such biases are necessary if the usefulness of regional collections is to be enhanced.

METHODS AND MATERIALS

Eleven species of Texas mammals, represented minimally by museum study skins, were recorded from the collections of Texas Tech University and Midwestern State University in March 1986. Specimens were categorized by month of capture (Fig. 1), and further subdivided into groups of those taken in the immediate vicinity of the respective institutions (herein defined as resident and immediately adjacent Texas counties) and those taken elsewhere in the state (Fig. 2). The TTU vicinity included Crosby, Floyd, Garza, Hale, Hockely, Lamb, Lubbock, Lynn, and Terry counties. Because MWSU is located in a county bordering Oklahoma, only the Texas counties of Archer, Baylor, Clay, Wichita, and Wilbarger were included.

Selection of Surveyed Species

We initially selected 11 taxa that were intuitively thought to be represented in each of the two collections by sufficiently meaningful sample sizes. The diversity of taxa was intended to reveal any subsequent biases due to variance of such factors as abundance, distribution, life history strategies, ease and means of collection and preparation, and storage space requirements.

Taxa also were chosen to represent mammals with known ranges that include all or part of the defined vicinity of each school (*Sylvilagus floridanus, Spermophilus tridecemlineatus, Dipodomys ordii, Peromyscus leucopus, Sigmodon hispidus*), and others that occur well beyond the vicinity of each (*Spermophilus variegatus, D. spectabilis, P. pectoralis*, and *Sigmodon ochrognathus*). *Myotis velifer* and *Bassariscus astutus* were included with the latter taxa because so few locally-taken specimens are available, although each is found in suitable habitats near each institution. Sources for distributional data were Dalquest and Horner (1984), Davis (1974), and Schmidly (1977, 1984).

Selection of Characters

Mammal specimens may be stored in a collection in various forms (for example, study skins, skulls, skeletons, fluid-preserved bodies, or in some combination of the above). The type of preparation may in part be biased to reflect the kinds of data desired by the collector or preparator. Therefore, even a numerically well-represented taxon may have limited use for some studies. For purposes of this study, we selected specimens prepared as museum study skins because this preservation technique is standardized among research collections and was therefore, expected to insure an adequate sample size.

RESULTS AND DISCUSSION

A distinct seasonal bias was noted in both collections surveyed (Fig. 1). For each of the 11 species examined, there was a preponderance of spring-taken animals. The summer months were most poorly represented. The two collections are to some extent complimentary. Individual assessment of the TTU and MWSU collections (Fig. 2) revealed contrasts in geographic biases for the five locally occurring taxa. Geographically, the MWSU collection is more heavily biased towards regional representation. Seasonally, the spring bias is particularly pronounced for MWSU specimens (Figs. 1 and 2).

Seasonal Biases

Regional mammal collections often are affiliated with colleges or universities. As a result, seasonal representation of taxa in these collections usually is reflected in the research interests of past and present workers and the academic calendar.

Biological or climatic phenomena often are related to unresolvable seasonal biases. Unfavorable environmental situations may elicit such responses as hibernation, aestivation, torpor, or migration, which directly affect the availability (even occurrence) of some mammals. Furthermore, seasonally inclement weather can preclude accessability to a region or simply discourage collecting efforts. Seasonal vegetation may lessen the attractiveness of trap bait or provide increased cover for some species, whereas others may be naturally cyclic in abundance.

Geographic Biases

Texas is a large and ecologically diverse state. It would be unreasonable to expect equal representation of each region in any collection of mammals. However, we would expect there would be a greater emphasis for locally collected animals than those taken from any other region in the state. With exceptions, we found this to be true (Fig. 2). From resident and adjacent counties of each institution, biases in representation also exist. MWSU is more heavily biased towards Wichita County, with lesser (but relatively balanced) collections from adjoining counties. Representation of local counties is more sporadic in the TTU collection. For the five locally occurring species examined, some counties are scarely represented, or not at all.

Geographic biases due to small sample sizes may result for a variety of reasons other than lack of collecting efforts. Species may be scarce or rare in some areas (for example, eastern Piney Woods, or South Plains

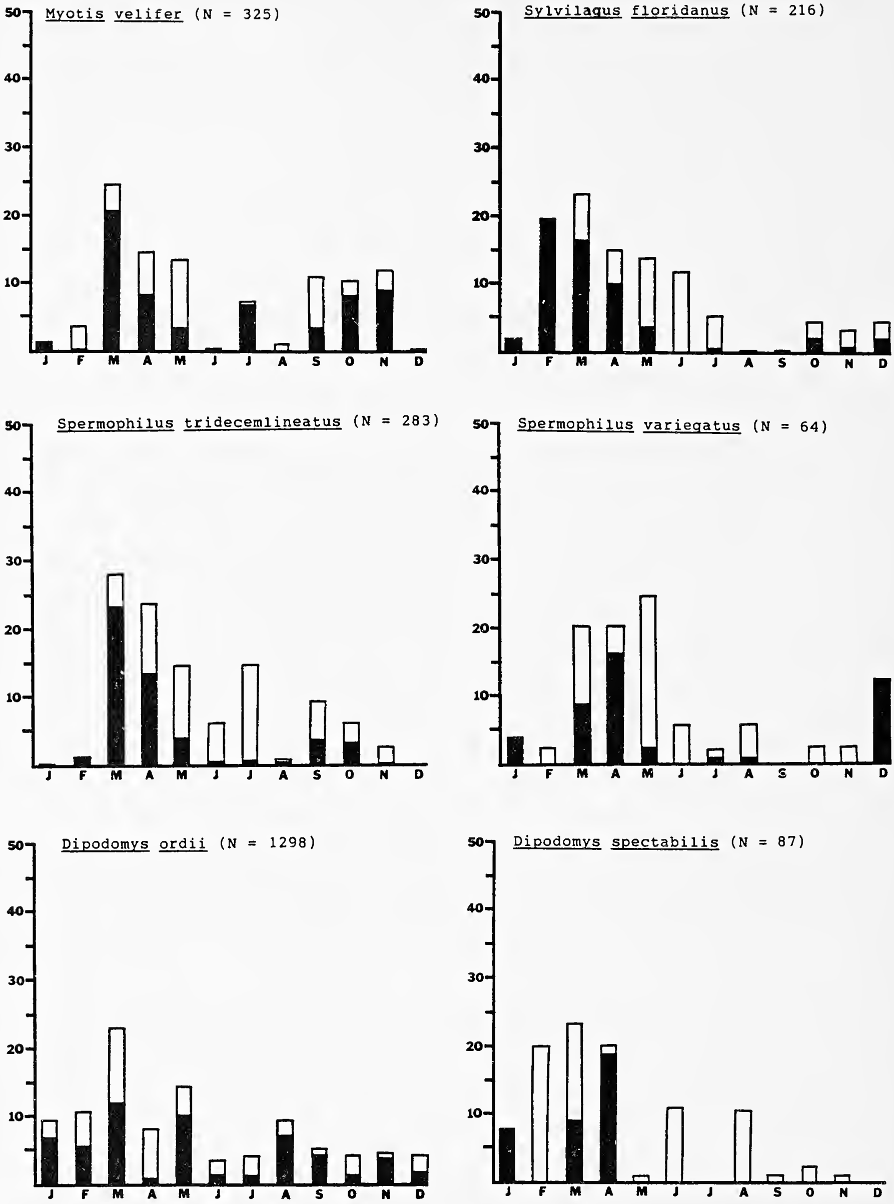

FIGURE 1. Histogram reflecting seasonal representation (percentages, by month) of 11 species of Texas mammals from the collections of Texas Tech University and Midwestern State University. Open areas of bars indicate TTU specimens; dark areas indicate MWSU specimens.

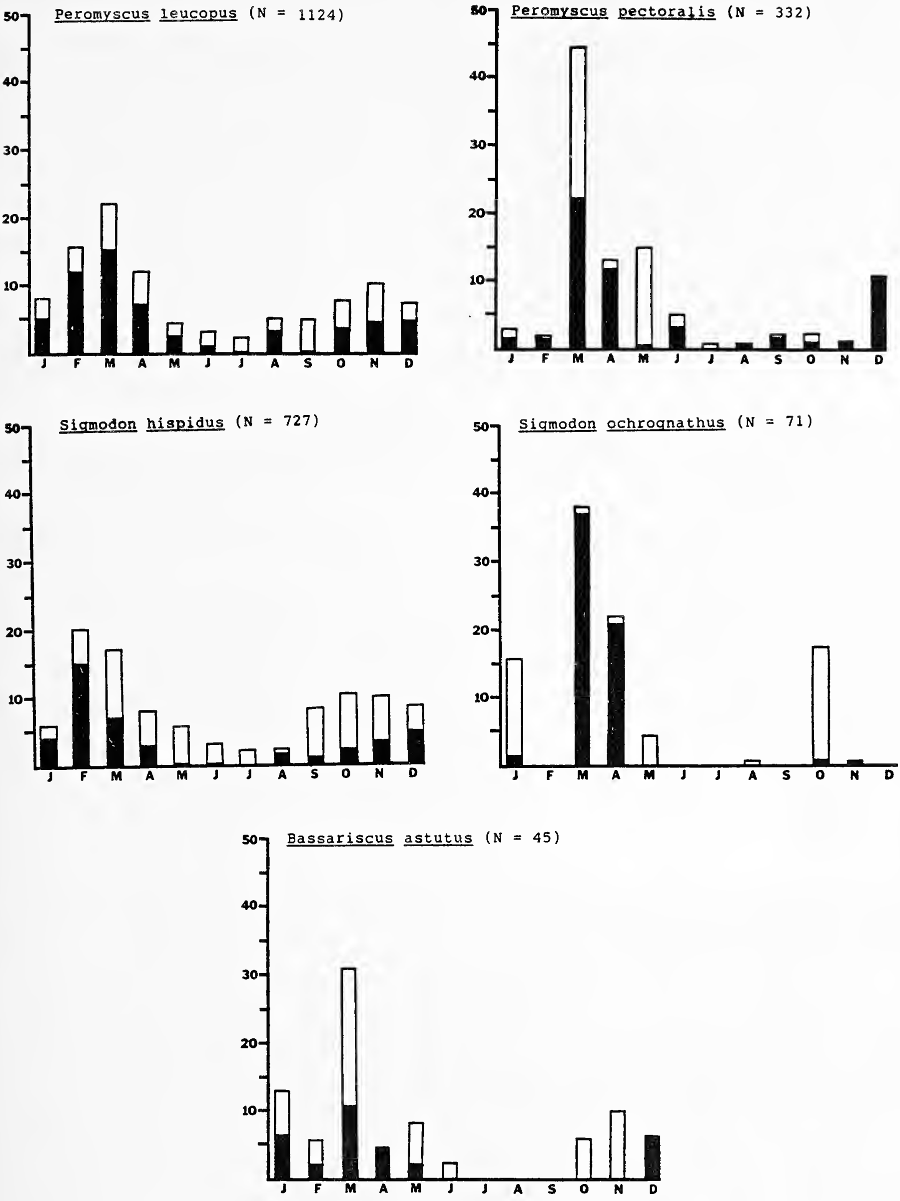

FIGURE 1. Continued.

agricultural counties) or throughout their range. Others may be more common than records indicate, but are not readily collected by usual means.

Because class field trips should be rewarding experiences for students, they often are planned with scenery and wildlife diversity in mind. For this reason, combined with past and present research interests, the Trans-

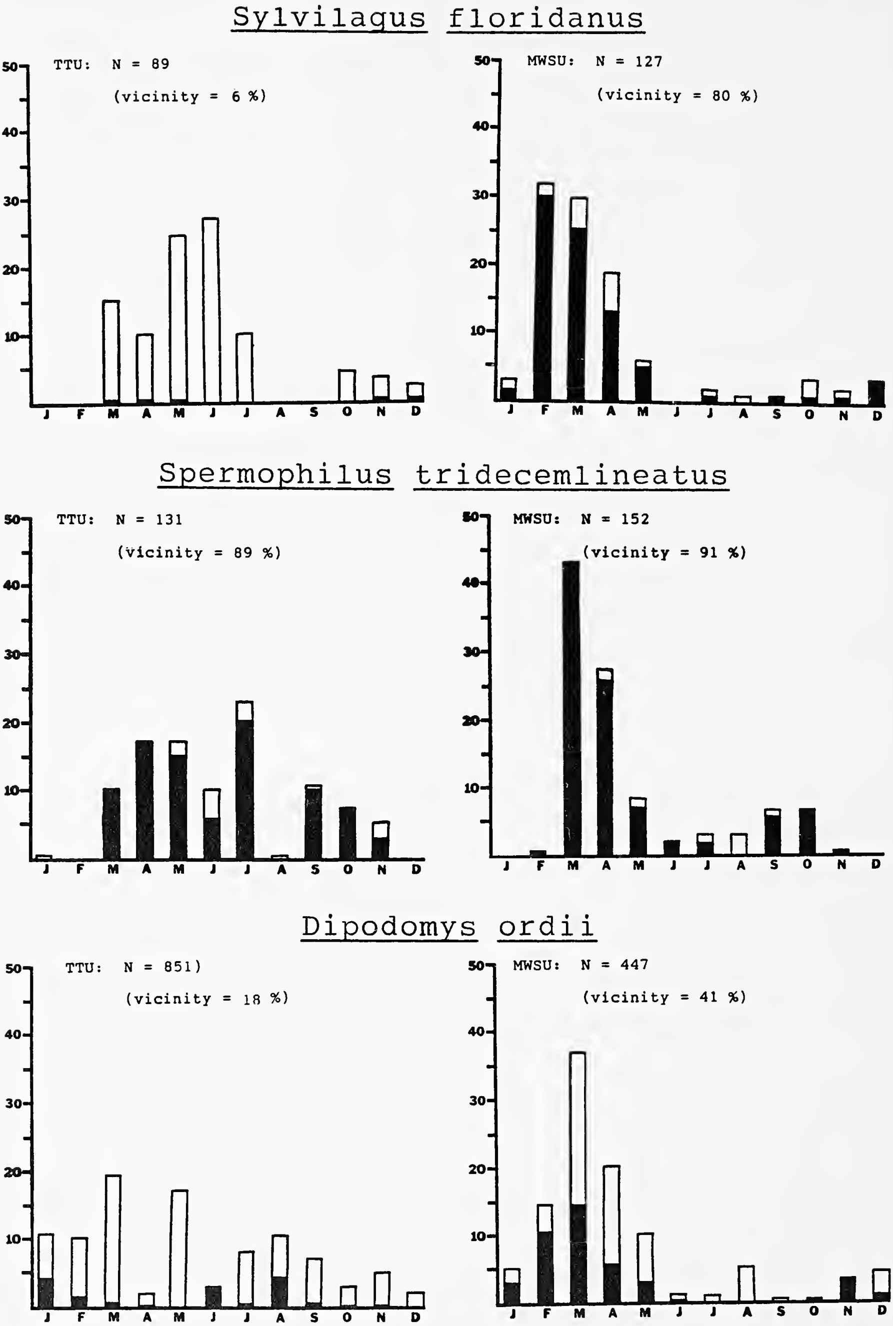

FIGURE 2. Histogram reflecting seasonal representation (percentages, by month) of five species of Texas mammals occurring in the vicinity of both Texas Tech University and Midwestern State University. Open areas of bars indicate specimens collected outside the defined vicinity of each school; dark areas indicate specimens taken in the vicinity of each school.

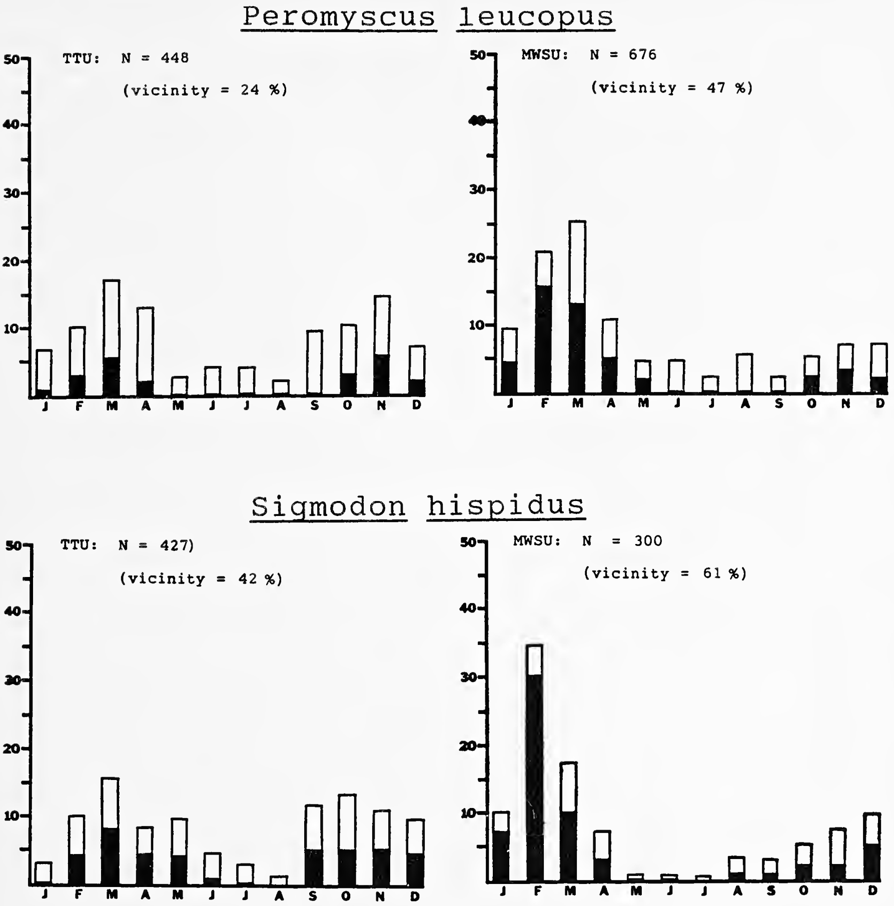

FIGURE 2. Continued.

Pecos is, aside from the local areas, the best represented region in both collections.

Addressing Collection Biases

For reasons discussed above, some biases are difficult and perhaps even impractical to alleviate. However, once recognized, others may be successfully addressed by the curator or collection manager.

The first step toward correcting, or at least minimizing, any collection bias is the identification of the gap in representation. Our methods were tedious and time-consuming, and dealt only with representation by museum study skins of 11 species. There is, however, a trend toward computerization of systematic mammal collections. The ease with which information retrieval is accomplished makes possible identification of any number of existing biases, thus proving an important curatorial tool in this respect.

Existing biases may be approached on a priority basis. Taxonomic gaps probably receive more attention than other biases; usually they are considered priority issues that can be remedied by specific collecting efforts or by exchanging specimens with other institutions. For seasonal and geographic biases, especially for locally occurring taxa, additional field collecting is the obvious solution. The following suggestions may be considered as possible solutions to better representation in collections.

If classes involving field collecting traditionally have been offered during the same semester, rescheduling of those classes may be possible. Planned field trips also may be scheduled at different times of the semester. Summer collecting with snap traps sometimes is undesirable, due to specimen spoilage and insect damage, and may, along with the academic calendar, contribute to the scarcity of summer-taken specimens noted in this study. The use of live traps will alleviate some of the problems.

It may be desirable to maintain some level of collecting locally the year around, if only for an occassional weekend. Emphasis could be placed on areas identified as geographically or seasonally underrepresented.

Collectors should assess their own prejudices. These are most likely expressed when more specimens have been taken than can be prepared. Juveniles often are discarded under such circumstances. Species that are large and require considerable storage space or are difficult to prepare (for example, lagomorphs and carnivores) are more likely to be represented by "skulls only." Others that are known to be abundant and widespread may be discarded (the "trash rat" designation). Although such taxa may be numerically well represented in a given collection, additional specimens may prove valuable if taken from certain localities or at certain times of the year.

Our study was a limited foray into determining the extent of seasonal and geographic biases of museum study skins in two systematic collections. While the existence of such biases may be anticipated, we feel the magnitude of some biases will surprise investigators who similarly evaluate their own collections.

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Current address of Jones: Department of Mammals, Transvaal Museum, P.O. Box 413, Pretoria, South Africa 0001.

A COMPARISON OF THE WATER CHEMISTRY AND BENTHIC MACROINVERTEBRATE COMMUNITIES OF TWO OXBOW LAKES IN THE RED RIVER BASIN, NORTHWESTERN LOUISIANA

Jack D. McCullough and Clarence W. Reed

Department of Biology, Stephen F. Austin State University, Nacogdoches, Texas 95962

Abstract.—The effects of periodic flooding by the Red River on two oxbow lakes were studied for one year. Wilson Lake was isolated from the river by a levee and was not flooded, whereas Old River Lake was connected to the river by a small channel. The two lakes were drastically different in both physicochemical conditions and benthic community structure. Wilson Lake was highly eutrophic, characterized by high phytoplankton production, BOD, ammonium nitrogen, orthophosphate, and color. High benthic standing crop and productivity, and low species diversity further reflect eutrophic conditions in Wilson Lake. Both lakes receive runoff from agricultural land. Occasional flooding of Old River Lake by the Red River appears to play an important role in the ecology of this oxbow lake. *Key words*: oxbow lakes; benthic macroinvertebrates; secondary productivity; water chemistry; species diversity; eutrophication.

Kalkomey (1979) pointed out that oxbow lakes are quite common in the Gulf Coast states, yet studies on those environments are relatively rare. Moore (1963) reviewed the literature on oxbow lakes in the central Gulf states and revealed that these typically are warm-water monomictic lakes (Moore, 1950; Geagan and Fuss, 1959) and typically support a high standing crop of plankton, benthos, and fish (Geagan and Allen, 1961; Lambou, 1960). Buckley and Sublette (1964) investigated the dipteran fauna of Cane River Lake, a lateral lake in Louisiana. Harrel (1973), Marsh et al. (1978), Reece (1979), and Kalkomey (1979) have conducted studies in oxbow lakes in eastern Texas.

Bingham (1969) found a high build up of insecticide in a Mississippi oxbow completely separated from the river, but such high levels were not found in a lake occasionally flooded by the river. The purpose of the present study was to investigate the importance of periodic flooding by the parent river on the water quality and the benthic community in oxbow lakes.

Study Area

The two oxbow lakes chosen for this study are cutoff meanders of the Red River in northwestern Louisiana (Fig. 1) and are relatively shallow, with depths only occasionally exceeding three meters. One of the lakes is connected to the parent river, whereas the other is isolated from river flooding by a levee.

Old River Lake is located in Natchitoches Parish, approximately 13 kilometers northwest of Natchitoches, Louisiana. The lake has a surface area of 72 hectares and is connected to the Red River by a narrow channel at the southern arm. Dominant land use around Old River Lake is agricultural, mainly cotton, although soybeans and other crops are produced

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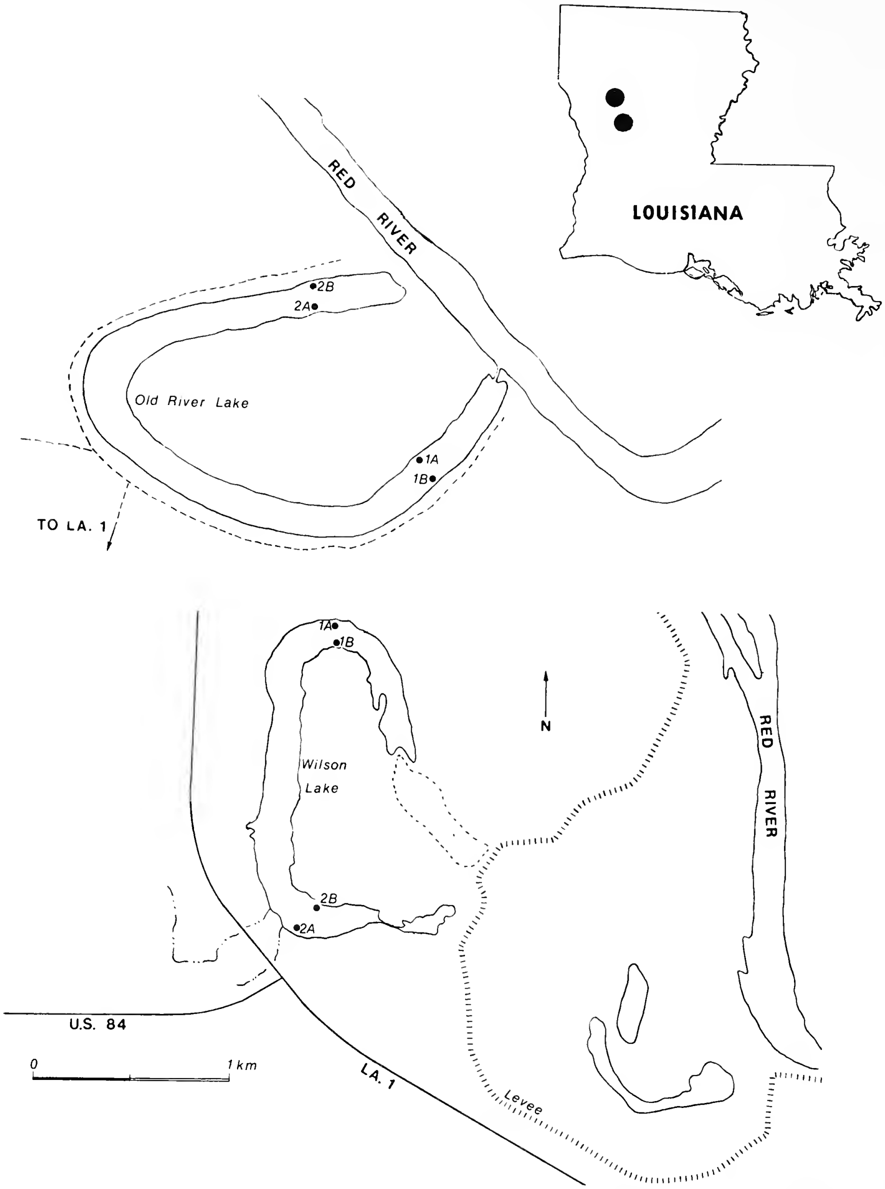

Figure 1. Old River Lake, Natchitoches Parish, and Wilson Lake, Red River Parish, in northwestern Louisiana, and location of collecting sites.

in the region. A majority of the shore line has a narrow band of trees, which supplies a considerable amount of detritus.

Wilson Lake is in Red River Parish, approximately 23 kilometers east of Mansfield, Louisiana. This lake has a surface area of 45 hectares and is completely separated from the river by a levee. Land surrounding the lake also is used for cotton and soybean production and for cattle pasture.

Each lake was sampled at four locations—one deep station and one shallow station near the end of each arm of the two lakes. Deep stations were given the letter designation A and shallow stations were designated B.

METHODS AND MATERIALS

Physicochemical Methods

Water for physicochemical analysis was collected monthly for one year from the surface at all eight sites and from one meter above the bottom at the deep stations. Samples were collected with a Kemmerer Water Sampler. Dissolved oxygen and conductivity profiles were done at each site using a Yellow Springs Oxygen Meter, model 54, and a Yellow Springs Conductivity Meter, model 33. Carbon dioxide and alkalinity were determined titrimetrically (APHA, 1980) in the field. Depth and Secchi disc transparancy also were determined at each station. Laboratory analyses were performed following procedures reported in APHA (1980). Colorimetric determinations were done using a Bausch and Lomb spectrophotometer, model 70. Phytoplankton chlorophyll *a* concentrations were determined on surface samples using a Turner flourometer, model 110.

Benthic Macroinvertebrate Methods

Benthic macroinvertebrates were collected monthly for one year at each collecting site using an Ekman dredge (231 square centimeters). At each site, five grabs were collected and pooled for analysis. Samples were washed in a benthic bucket having a no. 30 (0.59 mm) mesh screen bottom, then preserved in FAA (formalin-aceto-alcohol). In the laboratory, organisms were identified using keys by Edmunds et al. (1976), Edmondson (1959), Sublette (1964), Klemm (1972), Brown (1972), Mason (1973), and Pennak (1978).

The drained wet weight and dry weight of each organism (except entoprocts and ectoprocts) were determined using a Mettler analytical balance, model H10. Those weights were used to estimate secondary productivity by the size frequency method (Menzie 1980):

$$P_b = i \sum_{j=1}^{j} (\bar{n}_j - \bar{n}_{j+1}) \cdot (\bar{W}_j \cdot \bar{W}_{j+1})^{1/2}$$

where P_b is the biomass production per square meter per unit of time; i represents the number of size groups; $\bar{n}j$ is the mean number of organisms in size group j; and $\bar{W}j$ represents the mean weight of the size group j.

Species diversity was calculated for each sample using the Shannon equation (Shannon and Weaver, 1963):

$$\bar{d} = - \sum_{j=1}^{s} \left[\frac{n_i}{n}\right] \log_2 \left[\frac{n_i}{n}\right]$$

where $\bar{d}$ is the species diversity; n_i is the number of individuals of the ith taxon; and n represents the number of individuals of all taxa in the sample.

Statistical methods

The multivariate Hotellings T^2 and univariate t statistics (Dixon and Brown, 1979) were used to compare the physicochemical and benthic data between the two oxbow lakes. Pearson's correlation (Nie et al., 1975) was used to identify significant statistical correlations between chemical and biological parameters. Computations were done using a Honeywell CP6 mainframe computer.

TABLE 1. Annual means and ranges of physiochemical data on Wilson and Old River lakes, Louisiana.

	Wilson Lake			Old River Lake		
	Mean	Max	Min	Mean	Max	Min
pH	8.7	9.6	7.0	8.2	8.9	7.2
CO_2	3	15	0	2	5	0
HCO_3	77	115	9	108	114	63
CO_3	16	76	0	6	28	0
Turbidity (NTU)	9	43	1	5	17	1
Calcium	7	15	2	13	26	10
Sodium	14	17	11	16	19	14
Chloride	20	28	14	23	28	20
Iron	0.31	0.80	0.02	0.13	0.94	0.02
Sulfate	9	17	1	20	53	14
Ammonium-Nitrogen	1.07	2.12	0.58	0.59	1.54	0.16
Nitrate-Nitrogen	0.049	0.373	0.002	0.043	0.148	0.002
Total Kjeldahl nitrogen	4.86	10.81	1.4	3.21	7.24	0.74
Orthophosphate	0.311	1.02	0.07	0.194	0.58	0.04
Chlorophyll *a* (ug/L)	50	112	15	16	47	4
BOD	5.5	10.9	0.9	2.5	5.3	0.2
True Color (cu)	9	27	3	3	5	1
Apparent Color (cu)	23	98	8	11	24	2
Depth (meters)	2.6	4.2	2.3	2.1	3.4	2.0
Dissolved Oxygen	7.6	18.6	0.4	8.8	13.4	0.7
Conductivity (umho/cm)	237	329	190	278	338	210

All values are expressed as milligrams per liter except as indicated; pH units (1-14).

RESULTS

Physicochemical

Means and extremes values for physicochemical variables are given in Table 1. During the summer months, dissolved oxygen values in both lakes fell to less than one milligram per liter, but more often in Wilson Lake. Secchi disc transparancy was lower, whereas turbidity and apparent color values were higher in Wilson Lake. Ammonium nitrogen and orthophosphate were higher in Wilson Lake, but nitrate nitrogen concentrations were low in both oxbows. According to Carlson's Trophic State Index (Carlson, 1977), Wilson Lake was eutrophic and Old River Lake was mesotrophic. Using the index based on phytoplankton chlorophyll *a* values, Old River Lake had an index of 57 and Wilson Lake had a value of 69.

Benthic Community

A checklist of benthic organisms found in the lakes is given in Table 2. Average species diversity at Old River Lake was 2.14 and ranged from an average of 2.87 at 1B to 1.54 at 2A. Temporal variations in species diversity for each Old River Station are illustrated in Figure 2. The mean numerical density was 3723 organisms per square meter (org/m^2) ranging

TABLE 2. List of benthic macroinvertebrates collected from Old River Lake (O) and Wilson Lake (W), Louisiana.

Entoprocta	
Urnatella gracilis	O
Ecotprocta	
Fredericella sultana	O
Potsiella erecta	O
Plumatella repens	O
Oligochaeta	
Tubifex	O,W
Limnodrilus	O,W
Lumbriculus	W
Hirudinea	
Placobdella	O,W
Helobdella stagnalis	W
Helobdella sp.	O,W
Hydracarina	O,W
Amphipoda	
Hyalella azteca	O
Pelecypoda	
Sphaerium	O,W
Gastropoda	O,W
Ephemeroptera	
Caenis	O,W
Hexagenia	O
Odonata	
Perithemis	O,W
Gomphus	O,W
Megaloptera	
Sialis	O,W
Trichoptera	
Setodes	O,W
Orthotrichia	O
Coleoptera	
Haliplus	O
Dineutus	O
Berosus	O
Dubiraphia	O
Diptera	
Heleidae	O,W
Culicidae	
Chaoborus	O,W
Chironomidae	
Chironomus	O,W
Cryptochironomus sp.	O,W
C. edwardsi	O,W
Dicrotendipes	O,W
Einfeldia	O
Xenochironomus	W
Polypedilum	O,W
Lauterborniella	O,W
Microspectra	O,W
Coelotanypus	O,W
Tanypus	O,W
Procladius	O,W
Ablabesmyia	O

from 894 in March at Station 1A to 11655 in September at 1A. Average biomass was 2.92 grams wet weight per square meter (wet wt/m^2). Mean annual secondary productivity was 3.86 grams dry weight per square meter per year (dry wt/m^2/yr). The productivity of each station was 1A, 5.61; 1B, 1.68; 2A, 3.73; 2B, 4.41.

The culicid fly *Chaoborus* (Diptera) made up 39.7 percent of the benthic fauna at Old River Lake with an average of 1480 org/m^2, and 25.3 percent of the biomass or a mean biomass of 0.74 grams wet wt/m^2. Second to *Chaoborus* in numerical density were the chironomids, representing 33.7 percent of the numbers and 28.3 percent of the biomass. *Tanypus* (41.1 percent), *Procladius* (19.7), *Coelotanypus* (9.9), *Chironomus* (9.9) and *Cryptochironomus* (5.8 percent) were the most common genera collected.

Ceratopogonid larvae comprised 3.9 percent of the benthic fauna and 3.2 percent of the biomass with an average of 145 org/m^2 and 0.08 grams wet wt/m^2.

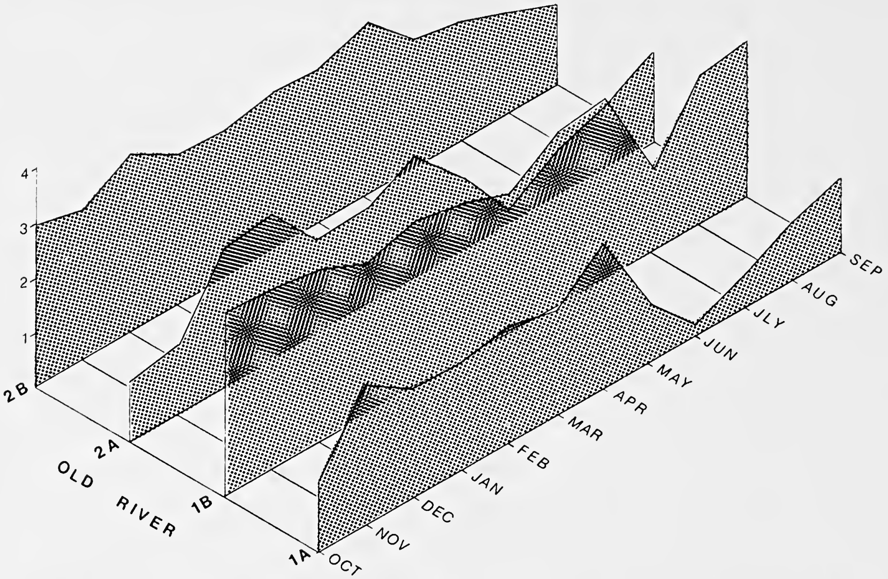

FIGURE 2. Monthly species diversity values for each collecting site on Old River Lake, Natchitoches Parish, Louisiana.

Members of the insect orders Ephemeroptera and Trichoptera accounted for only 2.7 and 1.2 percent of the total number of organisms collected at Old River Lake and 4.1 and 0.8 percent of the total biomass. *Caenis* was the most commonly collected mayfly, with an occasional specimen of *Hexagenia*. The caddis fly, *Setodes*, commonly was collected with occasional collections of *Orthotricha*. *Hyalella azteca* was the most commonly collected amphipod. Oligochaetes represented 15.1 percent of the organisms collected from Old River Lake and 31 percent of their biomass. Average numerical density was 560 org/m^2 and ranged from 3216 org/m^2 at station 1A in October to 43 at 2A in May. *Limnodrilus* accounted for 96.8 percent of the oligochaetes and *Tubifex* were collected only in small numbers.

Leeches were collected only at the shallow sites and represented approximately 1.5 percent of the population, with *Helobdella* and *Placobdella* being the most common genera.

The Odonata were represented in low numbers by the dragonfly naiads, *Perithemis* and *Gomphus*. The megalopteran alderfly, *Sialis*, was collected in low numbers on six occasions at 1B, and the elmid beetle, *Dubiraphia* (larvae), commonly was collected at the shallow stations only.

Urnatella gracilis, the fresh-water entoproct, was collected commonly at station 1B in numbers ranging from 26 colonies per square meter to 447 colonies per square meter. The ectoprocts, *Fredericella sultana,* *Pottsiella erecta*, and *Plumatella repens*, were collected only at stations 1A and 1B.

Mean species diversity at Wilson Lake was 1.72 ranging from an annual mean of 2.07 at station 1B to 1.35 at station 2B. Figure 3 illustrates the temporal variations in benthic diversity at Wilson Lake. Numerical density of the macroinvertebrates at Wilson Lake averaged 3815 org/m^2 ranging from 440 at 2B in May to 13,072 org/m^2 at 2B in October. Total biomass averaged 6.76 grams wet wt/m^2 with a minimum of 0.61 at 2B in September and a maximum of 18.35 at station 1A in January. The annual mean productivity was 9.56 grams dry wt/m^2/yr. The maximum rate was 14.76 at station 1B and the lowest 5.04 at station 2A.

Chironomid larvae were the dominant taxonomic group representing 37.1 percent of the total number and 53.7 percent of the biomass. Mean numerical density was 1416 org/m^2 and mean biomass was 3.63 grams wet wt/m^2. *Chironomus* accounted 38.6 percent of the chironomids collected at Wilson Lake, followed by *Tanypus* (25.1), *Procladius* (16.3) and *Coelotanypus* (14.8). *Chaoborus* larvae made up 27.5 percent (1050 org/m^2) of the total numbers but only 6.6 percent (0.45 grams wet wt/m^2) of the total biomass. Ceratopogonid larvae comprised 6.1 percent of the total numbers and 3.3 percent of the biomass at Wilson Lake.

Oligochates represented 25.9 percent of the benthic fauna of Wilson Lake with an annual mean of 987 org/m^2 and 26.8 percent of the biomass (1.81 grams wet wt/m^2). *Limnodrilus* accounted for 91.4 percent of the oligochetes collected, *Tubifex* accounted for 8.4 percent and *Lumbriculus* was present only in low numbers.

Leeches were found most commonly at Wilson Lake station 1B where they averaged 13.9 org/m^2. *Helobdella stagnalis* was most common followed by *Helobdella* sp. and *Placobdella*.

The pelecypod, *Sphaerium* (Sphaeridae), commonly was collected with an average population of 66 org/m^2 representing 4.0 percent of the total biomass. Water mites were frequently collected and the average density was 79 org/m^2. *Caenis* (Ephemeroptera), *Perithemis* (Odonata), *Sialis* (Megaloptera), and *Setodes* (Trichoptera) were collected on only a few occasions and only at station 1B.

DISCUSSION

Old River and Wilson lakes were different in both physicochemical nature and benthic community structure. Wilson Lake was a highly eutrophic lake characterized by high phytoplankton production, BOD, and color. High benthic standing crop, productivity, and low species diversity further reflect this highly eutrophic status. Runoff from agricultural land is thought to play a significant role in the eutrophication of Wilson Lake. Old River Lake was considerably less productive and classed as mesotrophic. Benthic

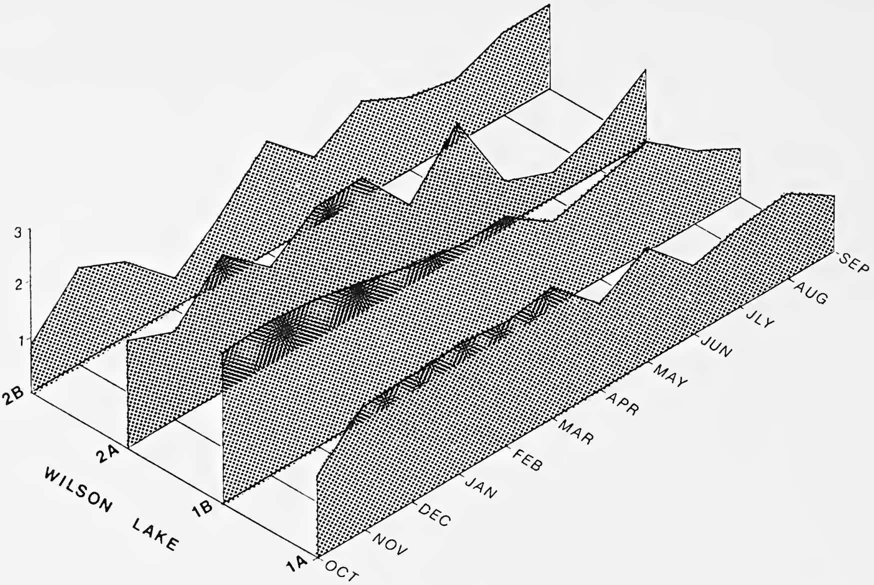

FIGURE 3. Monthly species diversity values for each collecting site on Wilson Lake, Red River Parish, Louisiana.

productivity was less than half, and average phytoplankton chlorophyll *a* concentration less than one third that of Wilson Lake. Benthic standing crop biomass at Old River Lake was significantly lower, whereas species diversity was significantly higher. Old River Lake also receives runoff from the cotton fields along the shoreline, but the Red River appears to play an important role in the ecology of this oxbow through occasional flushing of the lake by way of a narrow channel in the southern arm. When the river does not rise enough to flush the lake, the channel provides an outlet for excess runoff thus reducing the possible build up of nutrients, as in Wilson Lake.

Physicochemical Comparison Between Lakes

The means of all physicochemical parameters except temperature, and depth were simultaneously tested for equality between Old River and Wilson lakes using the multivariate Hotellings T^2 analysis. This statistic was found to be significant with $P < 0.001$. To determine which parameters contributed to this significance, two-sample t tests were applied to each parameter (Table 3). Using an alpha level of 0.05, 19 of the 22 means for chemical parameters were found significantly different between the two lakes.

Several parameters found in significantly higher concentrations at Old River Lake may provide evidence of the Red River's influence on that oxbow. Conductivity, calcium, sodium, sulfate, and chloride all were found

TABLE 3. Hotellings T^2 and two-sample t tests for selected chemical parameters of Old River and Wilson lakes, Louisiana.

	Hotelling T^2		1639.6		
	F value		62.9		$P < .001$

Parameter	t	p	Parameter	t	p
Secchi	9.60	<.001	PO_4	−4.85	<.001
oxygen	1.80	.075*	Chlorophyll *a*	−12.04	<.001
pH	−2.46	.015	Chloride	5.33	<.001
Conductivity	5.56	<.001	Turbidity	−3.18	.002
Calcium	6.48	<.001	BOD	−8.88	<.001
Sodium	7.26	<.001	HCO_3 Alk.	3.77	<.001
Sulfate	10.42	<.001	CO_2	−0.33	.740
NH_4-N	−9.63	<.001	CO_2 Alk.	−3.63	<.001
NO_3-N	−0.71	.481	True color	−9.44	<.001
NO_2-N	−1.71	.244	App. color	−6.40	<.001
TKN	−5.57	<.001	Iron	−2.36	.020

P values correspond to two-tailed tests of significance.
* one-tailed test is significant, $P = .0375$

to be significantly higher at Old River Lake. These parameters were reported in high concentrations in the Red River near Powhatan, Louisiana, by USGS (1980) (Table 4).

Secchi disc transparancy, color, turbidity, BOD, phytoplankton chlorophyll *a*, ammonium, and orthophosphate concentrations were all significantly higher at Wilson Lake, reflecting eutrophic conditions. Neither nitrate nor nitrite nitrogen was significantly different between the two oxbows. It is hypothesized, however, that the input of these nutrients into Wilson Lake was greater, but the higher input is rapidly utilized by the large algal population there. The accumulation of nutrients from agricultural runoff contributed to the higher ammonium and phosphate levels at Wilson Lake. Omernik (1976) found relatively high nutrient levels in streams draining agricultural land. Jones et al. (1976) found livestock as an identifiable source of phosphorus and ammonium-nitrogen within watersheds.

TABLE 4. Chemical data from the Red River near Powhatan, Louisiana, (USGS, 1980).

Parameter	Maximum	Minimum	Time-weighted average
Conductivity (umhos/cm)	1500	272	757
Calcium (mg/l)	109	27	51
Sodium (mg/l)	192	19	78
Sulfate (mg/l)	214	16	92
Chloride (mg/l)	290	28	123

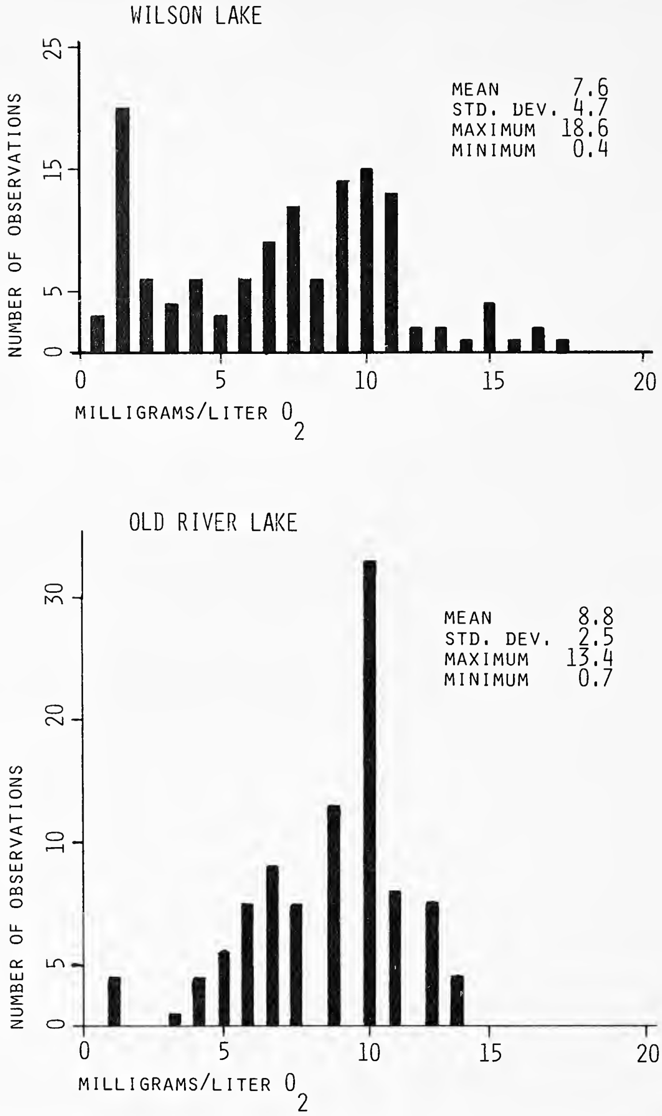

FIGURE 4. Histograms of monthly oxygen values at Old River Lake and Wilson Lake, Louisiana.

Although the annual mean for oxygen was slightly higher at Old River Lake, that difference was not significant. However, an inspection of a histogram (Fig. 4) of the distribution of the oxygen values recorded during the year at each lake reflects the more eutrophic conditions at Wilson Lake. There were several more oxygen values both in the low range and in the high range at Wilson Lake. Larger phytoplankton populations and respiration rates at Wilson Lake accounted for those differences.

TABLE 5. Hotellings T^2 and two-sample t tests for selected components of the benthic macroinvertebrate communities of Old River Lake and Wilson Lake, Louisiana.

	Hotelling T^2			128.5	
	F value			7.9	$P < .001$
Parameter	**t**	**p**	**Parameter**	**t**	**p**
Diversity	2.81	.006	Ephemeroptera		
Redundancy	−1.96	.053	numbers	2.38	.021
Oligochaeta			biomass	2.16	.036
numbers	−2.85	.006	Trichoptera		
biomass	−3.17	.002	numbers	3.03	.004
Chaoborus			biomass	3.49	.001
numbers	1.10	.275	All benthos		
biomass	1.48	.142	numbers	−0.20	.839
Chironomidae			biomass	−4.73	<.001
numbers	−0.52	.602			
biomass	−4.13	<.001			

P values correspond to two-tailed tests of significance

Benthic Macroinvertebrates

Differences in benthic macroinvertebrate community structure between the two oxbow lakes also were tested using Hotellings T^2. The statistic was significant with $P < 0.001$. Two sample t tests on each parameter revealed that species diversity, ephemeropteran and trichopteran numbers, and biomass were significantly higher at Old River Lake, whereas oligochaete numbers and biomass, chironomid biomass, and total benthic biomass were significantly higher at Wilson Lake (Table 5).

Species diversity was higher at Old River Lake indicating generally a less stressed environment than at Wilson Lake (Fig. 5). The low oxygen values often recorded for Wilson Lake were most likely a major contributing factor. However, species diversity index ranges reported by Wilhm and Dorris (1968) indicate that both oxbow lakes are moderately polluted. The greater abundance of tubificid oligochaetes at Wilson Lake is another indication of highly stressed conditions as members of the family Tubificidae are often found in large numbers in polluted areas (Goodnight, 1973).

A comparison of the chironomid populations at the two lakes reflects the differences in trophic conditions. *Chironomus*, a detritivore, and a genus associated with eutrophic lakes (Brinkhurst, 1974), dominated the chironomid populations at Wilson Lake. *Tanypus*, a hervivorus chironomid, and *Coelotanypus*, a predator, were the two most common chironomids in Old River Lake. Heuschele (1969) also found *Tanypus stellatus* to be the dominant benthic organism in a Minnesota floodplain lake. Numerically, chironomids were the dominant benthic organism in Wilson Lake, but the higher numbers were not statistically significant.

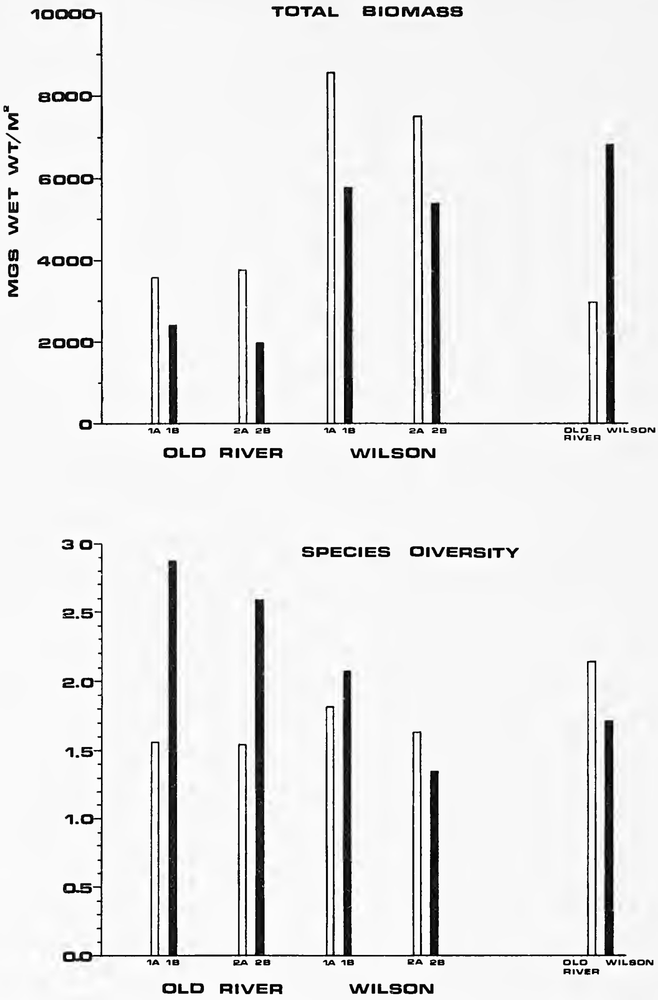

FIGURE 5. Average biomass and species diversity of the benthic macroinvertebrate community at collecting sites on Old River and Wilson lakes, Louisiana.

Large larvae of *Chironomus* accounted for the statistically higher chironomid biomass at Wilson Lake.

Both lakes had large populations of *Chaoborus punctipennis*, which was the numerically dominant benthic organism collected at Old River Lake. Again, numbers were not significantly higher. In both lakes, greater numbers of *Chaoborus* were found at the deeper sites at littoral stations. *Chaoborus* migrate vertically to deeper water during the day and return to the surface to feed (Welch, 1968). This behavioral mechanism probably allows the larva to avoid heavy grazing by planktivorous fish during the day. Lower numbers of *Chaoborus* in littoral areas in this study may be due to increased grazing by fish. Other reports (Paloumpis and Starrett,

TABLE 6. Comparison of annual benthic macroinvertebrate productivity (gms dry wt/m^2/yr) reported from several lakes.

P	Location	Source
27.5	Lake Taltowisko, Poland	Kajak and Rybak (1966)
21.3	Lake Mikolajskie, Poland	" "
12.5	Lake Sniardwy, Poland	" "
2.5	Lake Lusine, Poland	" "
1.9	Lake Flosek, Poland	" "
14.9	Lake Beloie, Russia	Borutzky (1939)
8.4	Wyland Lake, Indiana	Gerking (1962)
7.2	Linsley Pond, Connecticut	Deevey (1942)
6.9	Livingston Reservoir, Texas	McCullough and Jackson (1985)
5.7	Afon Hirant, N. Wales	Hamilton (1969)
3.1	North Lake, Texas	Durret (1973)
0.5	Fairfield Reservoir, Texas	Oliphant (1977)
10.0	Wilson Lake, Louisiana	This study
4.0	Old River Lake, Louisiana	"

1960; Harrel, 1973) also indicated that *Chaoborus* was predominantly found in deeper water of oxbow lakes during daylight hours.

Ephemeropteran and trichopteran numbers and biomass were significantly higher at Old River Lake, reflecting better water quality. Mayflies, caddis flies, and odonates rarely were collected in Wilson Lake and only at one collecting site (1B-a littoral area).

Benthic Productivity

Comparison of productivity of the benthic macroinvertebrates at Old River and Wilson lakes with several other reported values (Table 6) shows that the productivity of Wilson Lake is relatively high, whereas that of Old River is among the lower rates. Mann (1980) stated that the productivity of the benthic community was proportional to phytoplankton production rates. The phytoplankton standing crop was significantly higher in Wilson Lake, which would support that statement. However, Wilson Lake is thought to have the potential for higher benthic productivity, but is limited by extremely stressful conditions in summer. Northern lakes, without such stress during the growing season, are capable of much higher production provided other factors are not limiting. As Moore (1980) noted, algal availability is a key factor regulating invertebrate production in the temperate zone; however, benthic communities may be unable to take advantage of abundant algal growth in lakes where diversity is low owing to factors other than food supply. At Wilson Lake, where phytoplankton was always abundant, correlations between chlorophyll *a* and various components of the benthic community were extremely low. At Old River Lake, however, where chlorophyll *a* values were significantly lower, significant correlations were found between chlorophyll *a* and chironomid numbers ($r = 0.54$) and biomass ($r = 0.37$). The chlorophyll *a* correlation with *Tanypus*, a herbaceous chironomid, was 0.52, whereas the correlation with *Coelotanypus* (a predator) was −0.18.

In summary, periodic flooding or flushing of oxbow lakes by the parent river may reduce eutrophication of those lakes, at least along the Red River in the Gulf Coastal plains. The results of this study also suggest a mitigating factor in building impoundments on rivers. Releases from impoundments would flush oxbow lakes with relatively high productivity, reducing fertility and, in summer, those releases may reduce stress caused by low dissolved oxygen.

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EVALUATION OF VOLCANIC ASH AS A STRATIGRAPHIC MARKER IN PLAYA BASINS, WESTERN TEXAS

Kevin Cornwell and Calvin G. Barnes

Geotechnical Services, Inc., 5730 South 86th Circle, Omaha, Nebraska 68127, and
Department of Geosciences, Texas Tech University, Lubbock, Texas 79409

Abstract.—A volcanic ash deposit is exposed in Skeen Lake, a small playa basin in the larger Guthrie Lake basin on the Southern High Plains, Lynn County, Texas. The ash has been characterized to determine provenance and age. Characterization was accomplished through petrographic and major-element geochemical analysis. Bubble-wall and bubble-junction glass shard morphologies, average refractive index of 1.497, microphenocryst assemblage that included quartz, sanidine, magnetite, ilmenite, zircon, amphibole, clinopyroxene, allanite, chevkinite, biotite, and plagioclase, and distinctive concentrations of CaO (0.54 weight percent) and FeO (1.54 weight percent) helped "fingerprint" the ash. The ash is correlative with Lava Creek B ash deposits that originated in the Yellowstone area of Wyoming. This correlation suggests an approximate age of 621 thousand years (Pleistocene) for the Skeen Lake ash. Sedimentary features suggest several episodes of reworking and weathering during ash accumulation. *Key words:* volcanic ash; major-element concentration; shard morphology; microphenocryst assemblage.

Correlation of lacustrine sediments between playa basins on the Southern High Plains of Texas is difficult because correlation usually is based on the highly variable lithologic character of the sediments (C. C. Reeves, Jr., personal communication, 1983). Late Cenozoic volcanic ash deposits are preserved locally in some of these playa basins and respresent stratigraphic markers, age and source of which can be determined by laboratory study. Ash deposits can be used to correlate lacustrine sediments, estimate sedimentation rates, and provide minimum ages for these basins. Volcanic ash derived from eruptions at Long Valley, California (Izett et al., 1970; Borchardt et al., 1972; Kortemeier, 1982), Yellowstone, Wyoming and Idaho (Swineford and Frye, 1946; Izett et al., 1971; Naeser et al., 1973; Miller, 1974; Boellstorff, 1976), and the Jemez Mountains, New Mexico (Izett et al., 1972, and Izett, personal communication, 1984) have been recognized on the Southern High Plains.

Radiometric dating of ash deposits has been done by Evernden and Curtis (1951), Fleischer and Price (1964), Dalrymple et al. (1965), Naeser et al. (1971), and Boellstorff (1976). Dating techniques include fission track analysis of zircon, apatite, and glass and potassium-argon analysis of feldspar and biotite microphenocrysts. Uncertainties in such dates arise from counting statistics and also from problems related to deposition and sampling. For example, the abundance of radioactive minerals needed for radiometric dating is typically low in distal volcanic ash beds; thus, large

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quantities of ash are needed to concentrate a sufficient number of grains for analysis. In addition, post-depositional alteration can leach radioactive elements from the mineral to be dated and contamination can be introduced from detrital radioactive materials during reworking of the ash.

In order to overcome problems inherent in radiometric dating, it is possible to determine the geochemical characteristics of an ash unit and to match this "fingerprint" with volcanic source areas that have been dated previously. This technique has been an effective method for dating ash deposits on the Great Plains (Swineford and Frye, 1946; Czamanske and Porter, 1965; Theisen et al., 1968; Randle et al., 1970; Izett et al., 1970, 1971, 1972; Borchardt et al., 1972; Miller, 1974; Kortemeier, 1982; Izett, 1981) because the volcanic source areas generally lack detrital contamination and have fresh, abundant exposures.

The purpose of this project was to determine the geochemical characteristics of a volcanic ash deposit that occurs in the Skeen Lake basin and to determine the probable volcanic source and age. The ash should provide a useful stratigraphic marker in this and other Southern High Plains basins and its age provides constraints on the timing of basin formation. Such information is particularly important in view of the interest in siting a nuclear waste repository on the Southern High Plains (see Reeves and Temple, 1986).

METHODS

Field investigation incorporated drill hole and outcrop data in order to determine the stratigraphic relationship of the ash bed. Several pits were dug at various levels within the ash bed to reveal as much of the deposit as possible. Stratigraphic level was determined by tracing beds with oscillatory ripple marks.

A detailed petrographic inspection was conducted to determine glass shard morphologies and microphenocryst assemblage. Glass shards were separated from the ash using a water tower separation technique (Harris, 1965) and by hand picking. Immersion oils were used to determine the index of refraction of glass shards and the indices of immersion oils were checked using an Abbe refractometer with a sodium source. The microphenocryst assemblage was separated from the ash using the water tower apparatus, standard heavy liquid techniques, a Franz isodynamic separator, and hand picking. The microphenocrysts were identified using optical techniques.

Chemical compositions of individual glass shards were determined using a JEOL model JXA-733 electron microprobe at Southern Methodist University. The operating conditions were an accelerating voltage of 15 kilovolts, beam current of five nanoamps, and a beam diameter of 20 micrometers. The microprobe was calibrated using a suite of natural and synthetic standards.

STUDY AREA

The Southern High Plains of Texas are characterized by thousands of playa lake basins which range in size from several hundred square meters to several square kilometers. The playa basin chosen for this study is located in Lynn County, Texas, approximately 45 kilometers south of Lubbock, Texas, on U.S. Highway 87. At the time of this study, a small body of water (Skeen Lake) occupied this basin. The Skeen Lake basin is one of several small basins within the larger Guthrie Lake basin (Fig. 1). The Skeen Lake playa basin was selected for three reasons: 1) the occurrence of volcanic ash in the basin; 2) the relative abundance of ash (more than five meters thick in some areas); and 3) the accessibilility of the ash in drainage cuts and barrow pits.

Ash from two other Southern High Plains deposits, Buffalo Springs Lake in Yellow House Canyon, near Lubbock, and a playa basin approximately three miles south of Tulia, Texas, and pumice samples from the Jemez Mountains of New Mexico (Bandelier tuff) were collected for comparison with the ash in Skeen Lake basin.

In this report, the ash bed that underlies part of the Skeen Lake basin is referred to as the "Skeen Lake ash," the ash occurring in Yellow House Canyon is referred to as the "Buffalo Springs ash," and the ash that occurs south of Tulia, Texas is referred to as the "Tulia ash." These names are not formal stratigraphic terms, but serve to identify each of the deposits.

STRATIGRAPHY

An ash bed is exposed on the north and west sides of a small playa lake basin just north of Skeen Lake (Lynn County, Texas) in a man-made drainage cut and several barrow pits. The drainage cut is approximately six meters wide and 34 meters long and exposes the top 1.8 meters of the 5.2-meter-thick ash bed. Layering within the ash bed strikes N25W and dips one to four degrees to the northeast. A zone of white, calcareous sediment, 3.1 meters thick, occurs on the east side of the basin at approximately the same elevation as the ash deposit but does not contain ash.

A small power auger was used to drill two holes to determine the thickness of the ash deposit. One hole was drilled just north of the drainage cut and revealed an ash thickness of approximately 5.2 meters. The second hole was drilled in the floor of one of the barrow pits and approximately 4.6 meters of ash was encountered there. In both localities, the ash lies unconformably on the Duck Creek Formation of Cretaceous age.

Underlying Sedimentary Rocks

The Cretaceous Duck Creek Formation is a gray-green to yellow-brown sandy shale. Regionally, Cretaceous sediments are unconformably overlain by the Ogallala Formation. The conformity is typically exposed in larger pluvial basins such as the Gutherie Lake basin. However, erosion removed the Ogallala Formation from most of the Skeen Lake basin. Subsequent deposition and reworking of ash have complicated the unconformity by depositing ash directly on the Duck Creek Formation in peripheral parts of the basin but over lacustrine sediments in more basinward areas (C. C. Reeves, Jr., personal communication).

Skeen Lake Ash

Drill cuttings show that the lower 4.0 meters of the Skeen Lake ash is predominantly gray with cavities and solution channels filled with brown sediment (Fig. 2). The ash is fine grained and ranges in color from pale

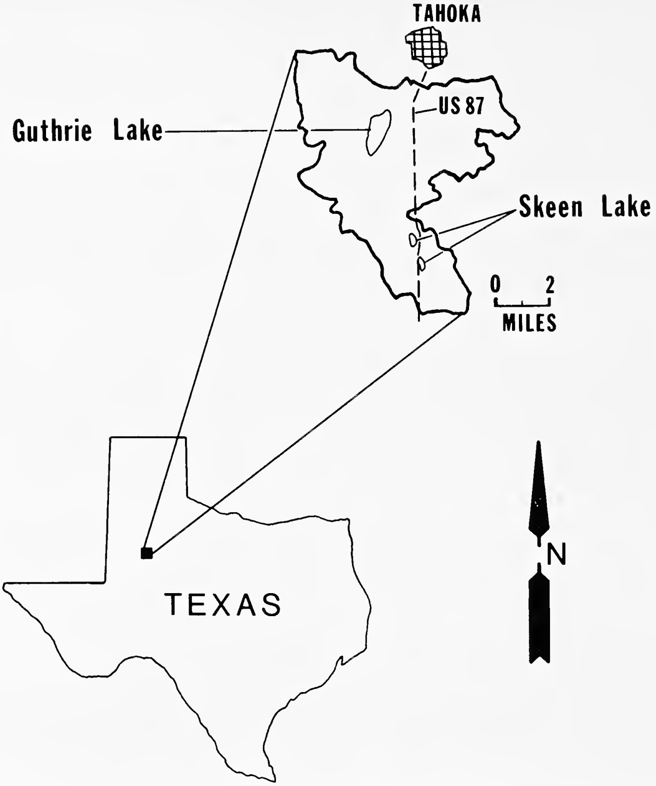

FIGURE 1. Location of the Guthrie Lake basin, Texas. Outline of the Guthrie basin shows the location of Skeen Lake and Guthrie Lake.

gray to gray. No phenocrysts are visible to the naked eye. Small (0.16 centimeter), black inclusions occur in isolated pockets and apparently represent organic material that was trapped in the ash during reworking of the initial airfall deposit.

Five fresh-water limestone lenses occur from 15 to 107 centimeters from the top of the unit. These limestone lenses are dark gray, indurated, discontinuous, and range in thickness from 0.3 to 3.8 centimeters.

At a height of 4.2 meters, oscillatory ripple marks occur and can be traced at least 24.4 meters. The ripple marks trend N89W, have an amplitude of about 0.65 centimeter, and a wavelength of 2.55 centimeters. In localities exposed to weathering, a layer of calcareous cement, 0.30 centimeter thick, caps the ripple marks.

Alternating layers of pale gray and gray ash occur above the ripple marks. Swirled flow structures, horizontal laminations, small (0.15 centimeter) black inclusions, and a small (2.5 centimeters thick) limestone lens all occur in this 20.3-centimeter section.

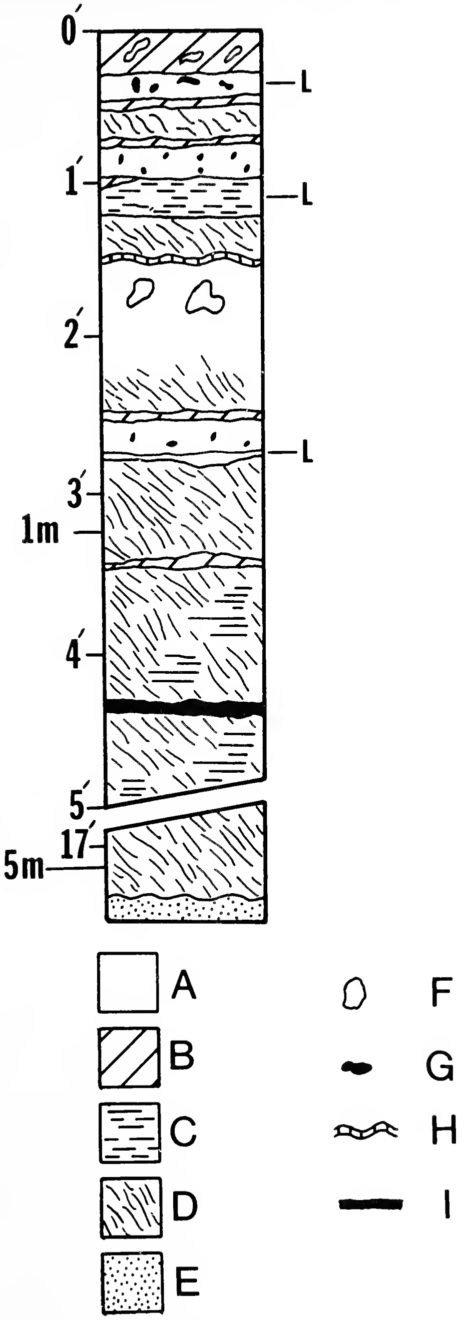

FIGURE 2. Stratigraphy of the Skeen Lake ash deposit. Ash is predominantly gray except as marked with (L), where it is pale gray. Units are: A, massive ash; B, calcareous ash; C, laminated ash; D, flow structure; E, Cretaceous Duck Creek Formation; F, pale gray ash zones; G, clay- and organic-rich pockets; H, oscillatory ripple marks; I, green ash.

The upper 23 centimeters of the ash bed represents the contact between ash and overlying sediment and are predominantly platy, calcareous, interbedded layers of pale gray and gray ash that range in thickness from 5.1 to 7.6 centimeters.

The most widespread bedding structures in the ash deposit are the swirled flow structures. These consist of thin parallel laminations contorted into swirls and circular shapes. Deposition by debris flow or sheet flow is the most likely explanation of these structures.

The presence of swirled flow structure in all sampled localities suggests that the process responsible operated on a basin-wide scale and was not restricted to one or two sites.

In the drainage cut, joints strike between N6E and N45E. These joints could be desiccation cracks or could be the result of loading and unloading forces caused by fluctuating levels of water in the basin. Thin (0.64 centimeter thick), white, indurated calcareous cement fills these fractures.

Discontinuous zones of weathered green ash occur at various locations within the deposit and are thought to represent hiatuses within the depositional cycles of the ash.

Weathered ash shows several diagenetic effects. In some localities a thin, white, indurated, calcareous layer plates the ash. In other localities, the upper eight to 15 centimeters of ash have become indurated with platy, calcareous cement. In barrow pits where the ash has been exposed to weathering for some time, it is yellowish green in color and is locally clay-rich.

Overlying Sediments

The ash is unconformably overlain by small (15 centimeters in diameter) discontinuous pockets of red-brown fine sand to sandy clay loam. Our work and more recent drilling by C. C. Reeves, Jr. (personal communication) show that these sediments are part of the eolian Blackwater Draw Formation (Reeves, 1976). Regionally, the Blackwater Draw Formation is permeated with white, semi-indurated caliche, which ranges in thickness from 15 to 76 centimeters and is overlain by soils from the Mansker and Portales Group (Mowery and McKee, 1958). These soils vary in thickness from 15 to 91 centimeters.

PETROGRAPHY

Shards comprise more than 99 percent of the ash and are composed of semihydrated optically isotropic glass. Shard morphologies are primarily bubble wall and bubble junction (approximately 96 percent) with the remainder being pumiceous. Heiken (1972) considered shard morphology to be governed by the viscosity of the original magma, which in turn is dependent on temperature, chemical composition, and volatile content (principally water and the halogens). Bubble-wall and bubble-junction shard morphologies are generally associated with magmas having relatively low viscosities, whereas pumiceous shards are characteristic of more viscous magmas (Izett, 1981).

Some of the glass shards appear slightly cloudy due to numerous gas bubbles. These gas bubbles are spheroidal in shape and are relatively abundant in the bubble-wall and bubble-junction shards. Rare shards are deep gray to black in color. Steen-McIntyre (1977) suggested that this phenomenon could result from exsolution of finely divided mafic minerals (for example, magnetite—Schlinger et al., 1986), or from contamination by magma mixing.

The refractive index of the glass shards ranges from 1.495 to 1.498 and averages 1.497. Refractive indices of glass shards from several ash beds on the Southern High Plains are shown in Table 1. Note that the refractive index of a glass sample depends, to a significant extent, on whether or not the glass is hydrated (Ross and Smith, 1955) because hydration tends to cause a change in refractive index.

The microphenocryst assemblage within the Skeen Lake ash bed is similar to assemblages in many other deposits on the Southern High Plains. Table 1 also shows the microphenocrysts that occur in ash deposits from several source areas. Note that the absence of plagioclase in the Bandelier tephra is considered to be characteristic of the unit (Izett et al., 1972) as is the occurrence of mica in the "Pearlette" ash. ("Pearlette ash" collectively refers to several ash beds that crop out on the Great Plains and were erupted from vents in the Yellowstone Park area.)

The microphenocryst assemblage of the Skeen Lake ash is quartz, sanidine, magnetite, ilmenite, zircon, amphibole, clinopyroxene, allanite, chevkinite, biotite, and plagioclase. Crystals that did not have glass adhering to their surfaces were classified as detrital grains although some may be microphenocrysts. Detrital grains were probably introduced during deposition and reworking of the ash.

In plane light, microphenocrystic clinopyroxene is dark green and slightly pleochroic. The Skeen Lake ash also contains detrital clinopyroxene that lacks adhering glass shards. The detrital clinopyroxene is pale green in color, diopsidic in composition, and has a sharp, angular morphology that suggests a minimum amount of abrasion during transport. The detrital clinopyroxene could have been entrained during eruption by erosion of the vent walls. Entrained xenocrysts would be transported and deposited with the ash but would not be cognate to the ash-forming magma and would lack attached glass. The pale clinopyroxene could also be tephra from a different (mafic) source area, such as New Mexico, Mexico, or Central America. If so, glass from such an eruption was not observed or has devitrified, leaving only its microphenocryst assemblage. No other angular microphenocryst phase lacking adhering glass was observed.

TABLE 1. Refractive indices of glass shards and microphenocryst assemblages from several Great Plains ash deposits.

Range	Average	Source
	"Pearlette" ash	
1.498-1.502	1.501	Swineford and Frye, 1946
1.499-1.501	N/A	Frye et al., 1948
1.498-1.500	1.499	Izett et al., 1970
quartz, oligoclase, sanidine, ferroaugite, hornblende, allanite, chevkinite, zircon, apatite, magnetite, ilmenite, sphene, mica, and clinopyroxene		
	Bishop ash	
1.492-1.499	1.495	Izett et al., 1970
biotite, hornblende, quartz, plagioclase, sanidine, zircon, apatite, allanite, sphene, ilmenite, and magnetite		
	Bandelier tephra (Guaje ash)	
1.497-1.499	1.497	Izett et al., 1972
quartz, sanidine, clinopyroxene, zircon, chevkinite, allanite, magnetite, and ilmenite		
	(Guaje pumice)	
1.496-1.498	1.497	Izett et al., 1972
	(Tsankawi pumice)	
1.496-1.498	1.497	Izett et al., 1972
	Mount Mazama	
1.501-1.518	1.508	Randle et al., 1970
plagioclase, hypersthene, magnetite, hornblende, clinopyroxene, trace apatite		

Allanite is yellow-brown to pale green in plane light. Allanite grains exhibit subhedral to anhedral morphologies and are the least abundant mineral present. Chevkinite occurs as long, pencil-shaped euhedral crystals and is red-brown in plane and polarized light.

Amphibole is dark brown to dark green in color and is anhedral. The anhedral morphology suggests resorption of amphibole by the host magma. Anhedral amphibole grains from other ash beds on the Great Plains have not been reported.

Garnet also occurs in the ash bed. The grains show little evidence of reworking and fluvial transport; however, the garnet grains are not attached to glass and are likely detrital. Izett (1981) noted that the occurrence of garnet in a magmatic suite probably is related to vapor-phase crystallization or incorporation of xenocrysts. Conversely, the garnet and diopsidic clinopyroxene could reflect detrital contamination from a high-grade metamorphic terrain (for example, the Sangre de Cristo Range, New Mexico).

Mineral assemblages separated from the Buffalo Springs and Tulia ashes and the Guaje and Tsankawi pumice beds of the Bandelier Tuff all contained quartz, sanidine, and clinopyroxene. Clinopyroxene similar to the detrital clinopyroxene in the Skeen Lake ash was not present in these ash and pumice beds. The Tulia ash contains rare anhedral amphibole but lacks magmatic biotite.

GEOCHEMISTRY

Most siliceous ash beds in the western and central United States can be classified as either rhyolitic or dacitic. Rhyolitic ashes can be further subdivided into G- and W-types. Izett (1981) showed that ash types also could be distinguished on the basis of shard types, mineralogy, glass composition, and refractive index. These features are summarized in Table 2. Izett (1981) showed that G-type and W-type rhyolitic centers are built on areas of continental crust that have undergone extensional deformation. These include Long Valley, California, Yellowstone, Wyoming, and the Valles Caldera, New Mexico. Dacitic centers typically are located near convergent plate margins such as the Cascade Range of the Pacific Northwest.

Major element compositions of glass from the three ash deposits under study are presented in Table 3. For purposes of correlation, elements that exhibit a noticeable degree of variation within and among tephra layers of different ages and origins are considered most useful. These elements are Ca, Fe, Mn, Mg, and Ti. Na and K are strongly affected by post-depositional diagenetic processes and yield results that are not characteristic of the original ash chemistry.

The Skeen Lake ash is clearly rhyolitic but does not exactly fit into either G- or W-type. However, the Skeen Lake ash shows greater similarity to G-type rhyolites than to W-type rhyolites, as is evident from its FeO content (Tables 2 and 3).

Average major-element concentrations of Skeen Lake, Tulia, and Buffalo Springs glasses and of tephra from other late Tertiary and early Quaternary volcanic systems are presented in Table 4. Comparison of FeO contents shows that the Skeen Lake and Tulia glasses are more FeO-rich than glasses from the Long Valley (Bishop), Los Chocoyos, or Crater Lake (Mazama) eruptive centers. CaO contents of the Skeen Lake and Tulia ashes are greater than those in Bandelier (Tsankawi and Guaje) eruptive products and less than those in Mazama and Los Chocoyos glass (Table 4). Both Skeen Lake and Tulia glasses are quite similar to glass from Yellowstone eruptive centers (Lava Creek B, Mesa Falls, and Huckleberry Ridge). The Lava Creek B glass most closely resembles the Skeen Lake and Tulia glass, suggesting that both of these playa lake deposits were erupted during the Lava Creek B event. Buffalo Springs ash is nearly identical to Guaje glass, supporting the correlation of the deposit with the Guaje eruption made by Izett (1981).

TABLE 2. Summary of the features of ash types (after Izett, 1981).

Ash type	Color	Distinctive shard type	CaO (wt. %)	FeO (wt. %)	SiO2 (wt. %)	Refractive index	Distinctive microphenocrysts
W-type	chalky	pumiceous	<0.55	<0.55	76-79	1.494-1.497	biotite, Na-poor sanidine
G-type	pale to med. gray	bubble wall and junction	<0.55	0.55-2.0	72-79	1.497-1.520	fayalite, Na-rich sanidine
dacite	white to grayish brown	complex	>0.55	>0.55	67-77	1.496-1.530	intermediate plagioclase

Table 3. Major-element compositions of glass shards from Skeen Lake, Tulia, and Buffalo Springs ashes.

	SiO2	A1203	FeO*	MgO	CaO	Na20	K20	Ti02	MnO	P205	Total
					SKEEN LAKE						
	72.05	11.36	1.63	0.03	0.45	2.96	5.24	0.16	0.12	0.14	94.14
	72.25	11.71	1.66	0.05	0.41	2.69	5.20	0.21	0.09	0.26	94.53
	72.33	11.42	1.25	0.03	0.57	2.71	5.06	0.14	0.00	0.06	93.57
	71.97	11.42	1.30	0.05	0.61	3.21	4.79	0.31	0.13	0.43	94.22
	71.11	11.39	1.33	0.04	0.55	2.88	5.38	0.26	0.11	0.14	93.19
	70.96	11.21	1.67	0.04	0.52	3.21	5.22	0.12	0.06	0.00	93.01
	72.98	11.60	1.14	0.04	0.47	3.26	5.17	0.17	0.00	0.00	94.83
	70.41	11.18	1.52	0.06	0.53	3.28	4.79	0.04	0.00	0.28	92.09
Ave.	71.76	11.41	1.44	0.04	0.51	3.02	5.11	0.18	0.06	0.16	
S.D.	0.73	0.15	0.15	0.01	0.04	0.29	0.18	0.05	0.05	0.05	
					TULIA						
	72.74	11.30	1.20	0.01	0.42	3.14	5.13	0.12	0.09	0.06	94.21
	70.83	11.14	1.61	0.06	0.47	3.02	4.75	0.14	0.01	0.33	92.36
	72.68	11.65	1.57	0.02	0.55	3.13	5.44	0.07	0.01	0.26	95.38
	71.81	11.27	1.52	0.02	0.57	3.14	4.81	0.21	0.10	0.13	93.58
Ave.	72.02	11.34	1.47	0.03	0.50	3.11	5.03	0.14	0.05	0.20	
S.D.	0.90	0.22	0.19	0.02	0.07	0.06	0.32	0.06	0.05	0.12	
					BUFFALO SPRINGS						
	72.21	11.69	1.04	0.02	0.17	4.13	4.59	0.17	0.07	0.12	94.26
	71.79	11.50	1.35	0.02	0.18	3.81	4.77	0.00	0.06	0.10	93.58
	70.96	11.16	1.29	0.01	0.23	3.53	4.86	0.00	0.12	0.00	93.68
	70.73	11.53	1.11	0.00	0.23	3.66	4.00	0.31	0.27	0.21	92.05
	70.51	11.16	1.25	0.02	0.11	3.54	5.02	0.04	0.00	0.31	91.96
Ave.	71.23	11.40	1.20	0.02	0.18	3.73	4.64	0.07	0.07	0.11	
S.D.	0.33	0.13	0.10	0.02	0.04	0.18	0.32	0.10	0.10	0.06	

*Total Fe as FeO

Environment of Deposition

The playa lake basin in which the ash occurs is located at the southeastern end of the much larger (approximately 16 kilometers long and eight kilometers wide) Guthrie Lake basin. Reeves (1966a, 1966b) suggested that many of the large pluvial lakes on the Southern High Plains were once part of an open lake system interconnected by early Pleistocene streams. These early Pleistocene drainage channels trend east to southeast (Gazdar, 1981). The lake basins formed over Cretaceous topographic highs where the Ogallala Formation was unusually thin. Once the drainage penetrated the Ogallala Formation and encountered the more competent Cretaceous shales and limestones, downward erosion slowed and lateral erosion predominated, carving out the lake basins.

The Guthrie Lake basin overlies Cretaceous sediment (predominantly Kiamichi Shale and Edwards Limestone) which, in areas surrounding the

TABLE 4. Major-element compositions of glass from selected pyroclastic rocks, normallized to 100 percent, anhydrous.

Ash	Age*	SiO2	A1203	FeO	MgO	CaO	Na20	K20	TiO2	MnO
1 Bishop Tuff	0.74	76.9	13.1	0.71	0.05	0.53	3.72	4.80	0.06	—
2 Bishop ash	0.74	77.3	13.0	0.72	0.07	0.56	3.43	4.80	0.07	—
3 Lava Creek B	0.61	76.8	12.2	1.57	0.02	0.54	3.57	4.98	0.10	0.01
4 Mesa Falls	1.27	76.8	12.2	1.49	0.04	0.58	3.21	5.41	0.11	0.03
5 Huckleberry Ridge	2.01	76.5	12.2	1.78	0.02	0.58	3.34	5.21	0.12	0.05
6 Skeen Lake	see text	76.7	12.2	1.54	0.04	0.54	3.23	5.46	0.19	0.06
7 Tulia	see text	76.8	12.1	1.64	0.02	0.56	3.25	5.47	0.14	0.04
8 Buffalo Springs	see text	76.9	12.3	1.30	0.02	0.19	4.03	5.01	0.08	0.11
9 Guaje ash	1.47	76.4	12.4	1.38	0.05	0.28	3.73	5.61	0.05	0.08
10 Guaje pumice	1.47	76.2	12.9	1.32	0.03	0.21	4.06	5.14	0.04	0.08
11 Tsankawi pumice	1.15	76.5	12.9	1.45	0.04	0.26	4.00	4.73	0.04	0.08
12 Los Chocoyos	85,000	77.0	12.9	0.90	0.31	1.18	3.98	3.60	0.14	—
13 Mazama	6,500	75.1	14.6	1.79	0.48	1.79	4.09	1.56	0.46	0.06

Sources for compositional data: 1 and 2 (Izett et al., 1970; 3, 4 and 5 (Christiansen and Blank, 1972); 6, 7, and 8 (this paper); 10 and 11 (Izett et al., 1972); 12 (Drexler et al., 1980); 13 Ritchey, 1980).

Sources for age data: see Table 1 in Izett (1981).

*Age in millions of years, except for Chocoyos and Mazama (in years)

basin, is unconformably overlain by sand and gravel of the Ogallala Formation. The age of the Guthrie Lake basin has not been clearly determined. Winkler (1985) considered the Ogallala Formation to be late Miocene-Pliocene in age. Thus the Guthrie Lake basin has a maximum age of mid- to late Miocene (assuming that the basin developed after the Ogallala Formation was deposited and did not exist during Ogallala deposition). In addition, the absence of sediments of Nebraskan and Kansan age in the basin suggests a late Pleistocene age (Fig. 2).

Because Quaternary drainage has been to the southeast, one would expect the deepest part of the Guthrie basin to develop in the southeast (that is, Skeen Lake basin). Numerous playa basins similar to the Skeen Lake basin occur within the Guthrie Lake basin, some of which are deeper than the Skeen Lake basin. However, the absence of ash in these playas suggests that they formed after the ash fall as the result of deflationary processes (Reeves, 1965) and are younger than the Skeen Lake basin. The occurrence of ash in the Skeen Lake basin and its absence from basins elsewhere within the Guthrie Lake basin may indicate that Skeen Lake was the only significant body of water present (in the Guthrie basin) during deposition and reworking of the ash, or that the major part of the Guthrie basin did not exist during early Pleistocene time. Outcrops of ash 4.6 to 6.1 meters above the present water level demonstrate that Skeen Lake was larger at the time of deposition than at present.

Discussion and Conclusions

Chemical analysis shows that glass from the Skeen Lake and Tulia ash deposits are compositionally similar to tephra erupted during the Lava Creek B event in the Yellowstone volcanic province (Table 4). This correlation is supported by the absence of Mesa Falls tephra elsewhere on the Southern High Plains (Izett, 1981). The Lava Creek B eruption occurred 610,000 years before present (see Izett, 1981). Thus the presence of this ash in the Skeen Lake and Tulia basins restricts basin formation to ages greater than 610,000 years.

In spite of the fact that older Pleistocene ash deposits occur elsewhere on the Southern High plains (Izett et al., 1972; Izett, personal communication, 1984), drilling shows that older ash does not occur in the Skeen Lake basin (Reeves, personal communication, 1986). With the exception of the Bishop ash, all of these eruptions were older than 1.15 million years (Table 4). Thus it is evident that the Skeen Lake basin formed in the interval between the last voluminous Bandelier eruption (1.15 million years) and the Lava Creek B eruption (610 thousand years). This interpretation is supported by the apparent absence of sediments of Nebraskan age in the basin. Further drilling within the Guthrie basin is necessary to confirm its chronology and the exact relationship to the Skeen basin.

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KARYOTYPES OF FIVE CRICETID RODENTS FROM HONDURAS

Robert D. Bradley and Jan Ensink

Department of Biological Sciences and The Museum, Texas Tech University,
Lubbock, Texas 79409, and Department of Biology, Texas A&M University,
College Station, Texas 77843

Abstract.—Karyotypes of five species of cricetid rodents (*Nyctomys sumichrasti florencei, Oryzomys cousei cousei, Peromyscus boylii sacarensis, Peromyscus mexicanus saxatilis*, and *Reithrodontomys sumichrasti modestus*) are reported for the first time from Honduras. The standard karyotypes of *Oryzomys cousei cousei* and *Peromyscus mexicanus saxatilis* revealed that these two subspecies possess the same diploid numbers as those previously reported for their respective species but possess different numbers of autosomal arms. The standard karyotypes of the remaining three taxa showed no variation from those initially described for their species. *Key words*: standard karyotypes; *Nyctomys sumichrasti; Oryzomys cousei; Peromyscus boylii; Peromyscus mexicanus; Reithrodontomys sumichrasti*; Honduras.

During a collecting trip to the Republic of Honduras, cricetid rodents were obtained from several localities and karyotyped. Among those collected were five subspecies for which the karyotypes, to our knowledge, have not been reported previously. Two of these subspecies had karyotypes that differed from those initially described for other races of the same species. The description of standard karyotypes of the five subspecies is the basis of this paper.

Materials and Methods

Somatic cell suspensions were prepared from bone marrow samples of wild-caught individuals as described by Baker et al. (1982). The frozen suspensions were thawed and standard metaphase spreads were prepared upon return to the laboratory. The descriptive morphology of chromosomes follows that of Patton (1967). The diploid number (2N) and total number of autosomal arms, designated as the fundamental number (FN), were determined for each taxon. Voucher specimens were deposited in the Texas Cooperative Wildlife Collections, Texas A&M University.

Results and Discussion

Oryzomys cousei cousei (Alston, 1877)

The karyotype (2N =56, FN =60—Fig. 1) of this taxon possesses three small biarmed pairs and 24 pairs of large to small acrocentric chromosomes. The X is a large subtelocentric chromosome; the morphology of the Y is unknown. This karyotype differs from that of *O. c. aquaticus* as reported by Benson and Gehlbach (1979) in that it has two additional biarmed pairs of autosomes. The X and Y were described as a large submetacentric chromosome and a medium-sized acrocentric or subtelocentric chromosome, respectively. The differences in FN and chromosome

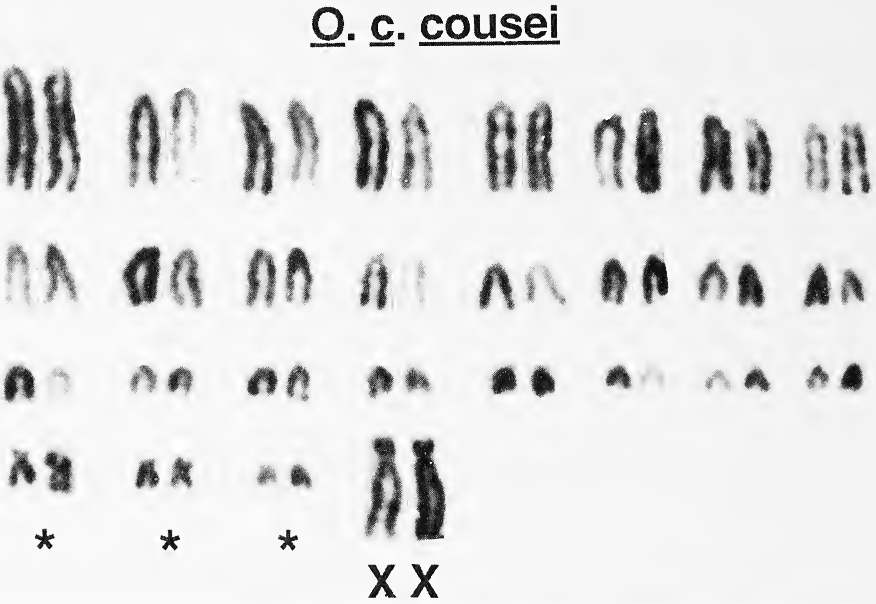

FIGURE 1. Standard karyotype of *Oryzomys cousei cousei*. Asterisks indicate biarmed autosomal pairs.

morphology of the biarmed pairs suggest that this karyotype is substantially different from that of *O. c aquaticus*; however, further investigations (differential staining techniques) are necessary to determine the significance of this variation.

Specimen examined.—Dept. Olancho: 2.4 mi. SW Dulce Nombre de Culmi, 1 ♀.

Nyctomys sumichrasti florencei Goldman, 1937

This karyotype (2N =50, FN =52) consists of one large and one small pair of biarmed chromosomes and 22 pairs of acrocentric chromosomes. The X is a large subtelocentric chromosome; the description of the Y is unknown as no males were examined. The karyotype of this subspecies is identical to that reported by Lee and Elder (1977) from Jalisco, México, for *Nyctomys sumichrasti sumichrasti*. Our purpose for reporting it stems from the fact that Honduras is a considerable distance geographically from Jalisco. This also represents the first reported karyotype for the subspecies, *N. s. florencei*.

Specimen examined.—Dept. Francisco Morazán: El Hatillo, 1 ♀.

Reithrodontomys sumichrasti modestus Thomas, 1907

This karyotype (2N=40, FN=76) possesses 38 metacentric to subtelocentric autosomes. The X is a large metacentric chromosome and

FIGURE 2. Standard karyotypes of *Peromyscus boylii sacarensis* (FN =52). Asterisks indicate biarmed autosomal pairs. The Y chromosome (from another individual) also is illustrated.

the Y is a medium-sized metacentric chromosome. The 2N =40 and FN =76 in this karyotype is similar to that reported by Carleton and Meyers (1979) and Hood et al. (1984) for *Reithrodontomys sumichrasti australis* from Costa Rica, but differs from the 2N =42 and FN =80 reported by Engstrom et al. (1981) for *R. s. nerterus* from México.

Specimen examined.—Dept. Francisco Morazán: 2 mi. NE El Hatillo, 1 ♂.

Peromyscus boylii sacarensis Dickey, 1928

The karyotype of this taxon (2N =48, FN =52 and 54—Fig. 2) exhibits a polymorphic condition in that three individuals examined possessed one large biarmed pair, two small biarmed pairs, and 19 acrocentric pairs of chromosomes (FN =52), whereas two other individuals possessed two large biarmed pairs, two small biarmed pairs, and 18 acrocentric pairs of chromosomes (FN =54). The difference between these two karyotypes involves a polymorphic condition (either an acrocentric or biarmed condition) for the second largest chromosomal pair. In both cases, the X is a large submetacentric chromosome, and the Y is a small metacentric chromosome. The polymorphism described herein is similar to that reported by Davis et al. (1986) and Houseal et al. (1987) for *P. b. beatae* (FN =48-54) from southern México. Although only the FN =52 and 54 conditions were apparent in this study of five individuals, a larger sample size should reveal mice with FN =53.

Specimens examined.—Dept. Francisco Morazán: 2 mi. NE El Hatillo, 1 ♂, 3 ♀; 1.3 mi. NE, 0.8 mi. E El Hatillo, 1 ♀.

FIGURE 3. Standard karyotype of *Peromyscus mexicanus saxatilis*. Asterisks indicate biarmed autosomal pairs.

Peromyscus mexicanus saxatilis Merriam, 1898

The karyotype (2N =48, FN =56—Fig. 3) of this subspecies is comprised of two large pairs, one medium pair, and two small pairs of biarmed chromosomes in addition to 18 pairs of acrocentric chromosomes. The X is a large submetacentric chromosome and the Y is a small metacentric chromosome. This karyotype differs from that originally described for *P. mexicanus* (Rogers et al. 1984) by possessing an acrocentric condition for the third largest pair of chromosomes instead of a submetacentric condition. This acrocentric condition results in a FN =56 rather than the FN =58 as described by Rogers et al. (1984).

The FN =56 condition of *P. m. saxatilis* is not only unique to *P. mexicanus*, but is unique to the entire *P. mexicanus* group, because the nine species of this group previously studied all have a karyotype of FN =58 (Rogers et al., 1984; Smith et al., 1986).

Specimens examined.—Dept. Francisco Morazán: 6 mi. NE El Hatillo, 2 ♂, 1 ♀, 1.3 mi. NE, 0.8 mi. E El Hatillo, 1 ♂, 2 ♀.

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FRESHWATER BIVALVES OF THE BAFFIN BAY DRAINAGE BASIN, SOUTHERN TEXAS

RAYMOND W. NECK

Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744

ABSTRACT.—The freshwater bivalve fauna of the streams draining into Baffin Bay in southern Texas consists of six species of unionids and the introduced Asiatic clam. Although all of the unionids are native to southern Texas, only one species is believed to be native to the drainage basin of Baffin Bay. *Key words*: freshwater bivalves; Baffin Bay, Texas.

The coastal plain of Texas is drained by a series of rivers ranging from the Sabine River on the eastern boundary to the Rio Grande on the southwestern boundary. A relatively large area north of the Rio Grande drainage and south of the Nueces River contains no sizable drainages. The southern part of this area is known as the Llano Mesteño. No cohesive drainages occur on the Llano, the northern area of which contains a series of intermittent streams that flow into a hypersaline estuary known as Baffin Bay (Fig. 1).

Limited biological surveys have been carried out in this area of southern Texas, and no freshwater mussels have been reported from the study area (Strecker, 1931). Herein are reported the results of a survey to determine the distribution of freshwater mussels of this region. Regional studies of mussel faunas have covered the Nueces system (D. W. Taylor, unpublished data) and the lower Rio Grande (R. W. Neck and A. L. Metcalf, unpublished data).

The environment is moderately xeric. Rainfall is moderate (average annual total for Kingsville is 628 mm), but temperatures are also high (average temperatures for January and July are 13.3°C and 28.9°C, respectively). Most of the streams are intermittent in flow; low runoff periods wash out salt accumulations (Simmons, 1957), whereas torrential runoffs following tropical depressions may scour out normally stable creek bottoms (Suhm, 1974; Russell and Wood, 1976). Some evidence exists that the climatic regime has become more xeric during the past 150 years, but the natural tendency toward low, irregular flows in area creeks may have been exacerbated by land use policies—for example, land clearance for farming, damming of certain streams as stock tanks for ranching, and withdrawal of ground water for municipal and industrial use (Bollaert, 1850; Price and Gunter, 1942). Geological evidence indicates that an extensive river system with moderate water flow occurred in this area during the late Pleistocene (Suhm, 1978). Water pollution is slight to moderate and involves sewage, pesticides, herbicides, and industrial sources (Breuer, 1957).

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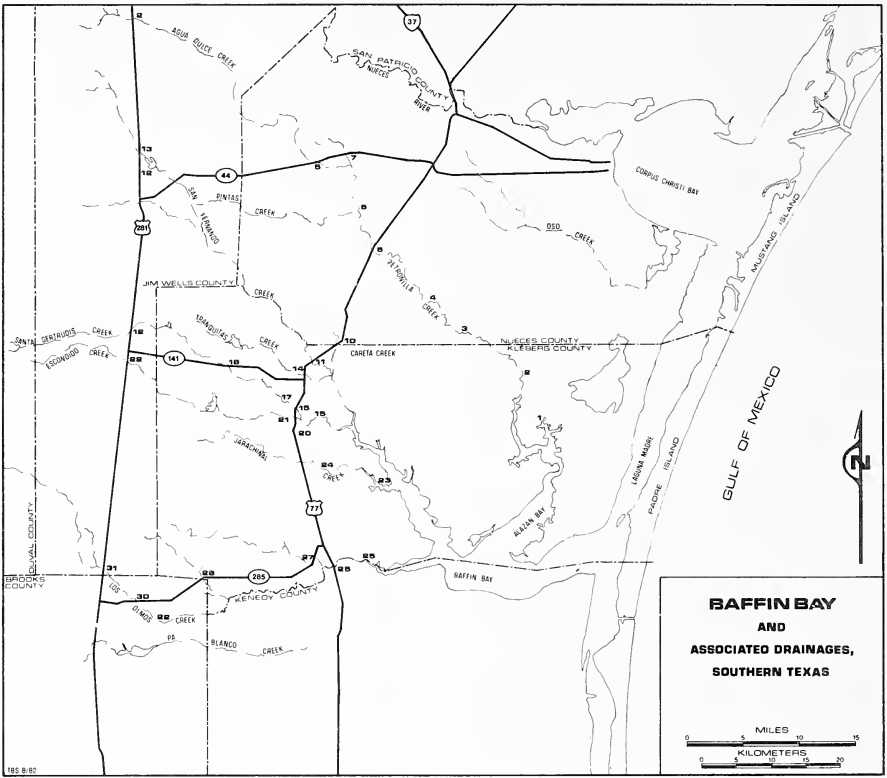

ADAPTED FROM GEOLOGIC ATLAS OF TEXAS, UT BEG 1975/76

FIGURE 1. Map of drainages of Baffin Bay, Texas, with sampling localities for freshwater bivalves.

BIVALVE FAUNA

Comprehensive field sampling over the drainage area of Baffin Bay has revealed a highly localized, low-diversity freshwater mussel fauna. Of 31 sites surveyed, only five supported populations of freshwater bivalves (Table 1). Voucher specimens have been deposited in the Dallas Museum of Natural History.

Anodonta imbecilis Say, 1829.—This small, thin-shelled mussel is known from a single pond (locality 6) in the study area. Shells have a brown periostracum with few or no green rays or suffusion. This population is probably referable to the central Texas subspecies *A. i. horda* (Gould, 1855).

Quadrula apiculata speciosa (Lea, 1862).—For many years, Texas populations were referred to under the names *Quadrula quadrula* (Rafinesque, 1820) or *Q. q. apiculata* (Say, 1829). A single valve of this species was found in Dairy Lake (locality 18). Pustules are reduced in height above valve surface and are less common on peripheral areas of the shell.

TABLE 1. Distribution of freshwater bivalves of Baffin Bay drainage area by habitat, southern coastal plain of Texas.

Species	Fresh creek	Salt creek	Fresh pond	Estuarine	Total
Anodonta imbecilis	-	-	1	-	1
Quadrula apiculata speciosa	-	-	1	-	1
Uniomerus tetralasmus	2	-	2	-	4
Cyrtonaias tampicoensis	-	-	1	-	1
Lampsilis teres	-	-	1	-	1
Toxolasma texasensis	-	-	3	-	3
Corbicula fluminea	-	-	2	-	2
Sites with bivalves	2	0	3	0	5
Total sites	11	10	6	4	31
Total species	1	0	7	0	7

The shell resembles those of *Q. a. speciosa* (Lea, 1862) from the Nueces River and the Rio Grande.

Uniomerus tetralasmus (Say, 1831).—This species is the most widely occurring and abundant clam in the Baffin Bay drainage area (localities 6, 8, 11, 18). Creek specimens are only moderate-sized, reaching a shell length of 78.9 mm. Lake specimens reach a greater length (up to 121.2 mm) and develop a rounded ventro-posterior tip as the posterior ridge becomes noticeable. Nacre color is white. The above characters indicate *tetralasmus* as the proper assignment according to analyses by Frierson (1903) and Morrison (1977). Both of these authors concluded that *Uniomerus declivus* (Say, 1831) and *U. tetralasmus* are valid species whereas Johnson (1970) synonymized the two taxa.

Cyrtonaias tampicoensis (Lea, 1838).—Shells of this species were found only in Lake Alice (locality 12), an artificial impoundment in the San Fernando Creek system. Several individual valves and one articulated pair were found in one area three meters in diameter. The intense localization of shells and absence of small individuals suggest strongly that these represent animals imported for use as fish bait. A likely source is the Nueces River (especially Lake Corpus Christi) to the north. No evidence of an established breeding population was uncovered. The recovered shells formerly were referable to *C. berlandieri* (Lea, 1857), which is either synonymous with, or a subspecies of, *C. tampicoensis*.

Lampsilis teres (Rafinesque, 1820).—Individuals of this species from a single site (locality 6) are rather thin-shelled and have green rays. No infraspecific epithet is deemed appropriate at this time because the green-rayed character may be a unifactorial genetic polymorph. For many decades this species was referred to as *L. anodontoides* (Lea, 1831), but Johnson (1972) pointed out that *teres* has priority. The rejection of *teres* by Pilsbry (in Ortmann and Walker, 1922) as "not identifiable" was due to "specious reasons" according to Johnson (1972).

Toxolasma texasensis (Lea, 1857).—For many years this taxon was referred to the genus *Carunculina* Simpson, 1898. Recently, Valentine and Stansbery (1971) utilized *Toxolasma* Rafinesque, 1831, because it is an older name (Morrison, 1969). Shell characters discussed by Valentine and Stansbery (1971) indicate that the species present in the Baffin Bay area is *texasensis*. Shells are moderate in size (length to 49.6 mm) with a peach-colored nacre. Assignment of a subspecific name would be premature at this time. Names available from southern Texas (all type localities in the Rio Grande drainage) include: *Unio bairdianus* Lea, 1857; *Lampsilis texasensis compressus* Simpson, 1900; and *Lampsilis mearnsi* Simpson, 1900.

Corbicula fluminea (Müller, 1774).—The Asiatic clam was found only in two lake environments (Lake Alice and Dairy Pond). Individuals of this species were not common at either of these localities; most shells were from 35-40 mm in length. While the restricted size also could indicate a nonbreeding introduction, a more likely explanation involves the rarity of successful spawning. Shells found in the study area have a pale purple nacre and pale honey-brown periostracum. All *Corbicula* from the Baffin Bay drainages are referable to the "white form" of Hillis and Patton (1982).

DISCUSSION

Field surveys have revealed an isolated, low-density bivalve fauna of low species diversity inhabiting the creeks and ponds (stock tanks) of the Baffin Bay system. Low precipitation and a high evaporation rate produce intermittent streams in areas of soft sediments. Analysis of the collecting sites as to habitat type reveal that all species were found in freshwater ponds; only one, *U. tetralasmus*, was found in freshwater creek habitats (Table 1). This distributional pattern indicates the likelihood that all mussel species recorded from this area are introduced except for *U. tetralasmus*, a species that is rare in both the Nueces and Rio Grande systems. Introduction of the other species probably occurred via introduced fish stock. Although *U. tetralasmus* is well adapted to periodic desiccation, murky water, and soft substrates, this species was conspicuously absent from Lake Alice (locality 12). In fact, Lake Alice was the only site with mussels that did not support a population of *U. tetralasmus*. This species, however, does not appear to adapt well to large bodies of permanent water (Murray, 1979).

The portion of southern Texas that is drained by streams flowing into Baffin Bay can be divided into three broad zones in reference to general suitability of the environment for freshwater bivalves. A coastal zone (inland to an approximate elevation of 28 meters above mean sea level) is characterized by salinity levels sufficient to cause soil precipitate. Freshwater bivalves might be able to live there for short periods of time in temporary freshwater ponds following heavy rainfall. A middle zone (between 16 and 28 meters above mean sea level) exhibits salinity levels that do not result insoil precipitate, but streams in this zone have frequent periods of no flow. An inland zone (generally above about 28 meters mean sea level) is characterized by tolerable salinity levels, although water is still rather scarce. This inland zone also contains large stock tanks that support populations of the locally introduced unionid species and the Asiatic clam. The inland zone also may experience lower rates of siltation due to slightly higher elevation (yielding more rapid water movement) and greater percentage of pasture land as opposed to cultivated land (yielding less silt because of vegetation cover).

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EFFECT OF SALT ON GRAIN AND FORAGE INTAKE IN CATTLE

Robert D. Brown and Alejandro Creixell
Caesar Kleberg Wildlife Research Institute and College of Agriculture and Home Economics, Texas A&I University, Kingsville, Texas 78363

Abstract.—Grain rations containing 0, 20, 30, 40, or 50 percent salt were offered to 15 steers receiving chopped coastal Bermuda grass (*Cynodon dactylon*) or Kleberg bluestem (*Dichanthium annulatum*) hay ad libitum. Grain intake ($DMI/BW^{0.75}kg$) decreased ($P < .01$) with the addition of salt, but there was no difference ($P > .05$) in grain intake between salt levels. The overall salt intake was 0.189 percent (SE = 0.016) of body weights. The effect of salt on grain intake for cattle receiving coastal Bermuda grass hay was predicted by the equation $DMIg/BW^{0.75}kg = 0.148 - 0.060\ (\%\ NaCl) + 0.007\ (\%\ NaCl)^2$, $R^2 = 94.98\%$; whereas that of cattle receiving Kleberg bluestem hay was predicted by the equation $DMIg/BW^{0.75}kg = 0.151 - 0.053\ (\%\ NaCl) + 0.005\ (\%\ NaCl)^2$, $R^2 = 92.4\%$. Intake of coastal Bermuda grass was higher ($P < .01$) than that of Kleberg bluestem when hays were fed alone. Cattle consuming grain ate less ($P < .05$) hay than those not receiving grain. There was no difference ($P > .05$) in hay intake ($DMI/BW^{0.75}kg$) between cattle receiving any grain ration. Cattle overconsumed grain when grain was not salted. At salt levels above 20 percent, intake of the hay-grain mixes was inadequate to meet requirements. It is thus recommended that salt should not be added to grain rations above 20 percent to limit grain intake in beef cattle. *Key words*: salt; livestock; supplement; feed; digestibility.

In areas where forages tend to be of low quality, the use of supplemental feeds for beef cattle is a necessary practice. However, supplements commonly are expensive, and the daily feeding of range cubes or grain mixes is labor intensive. Sodium chloride (NaCl) frequently has been used to regulate the intake of supplements provided free-choice to cattle on rangelands (Weir and Torrel, 1953; Riggs et al., 1953; Cardon, 1953). The advantages of feeding salted grains to cattle are that overconsumption can be controlled, supplement for several days can be placed in self-feeders, and labor can be reduced (Cunha, 1980). Unfortunately, salt also can be toxic if consumed in excessive amounts. Surprisingly little research has been done on the specific percentages of salt required to reduce grain intake in beef cattle (Morris, 1980).

The objectives of ths investigation were: 1) to determine the consumption of concentrates and forages by beef cattle at various levels of NaCl for two forages; and 2) to generate a regression equation for each forage to predict grain intake at different salt levels.

Materials and Methods

The experimental facility consisted of an open pen, 30 meters long by 12 meters wide, with a three-sided shed at the north end housing 16 electronic feeding gates (Calan Broadbent Inc., Northwood, New Hampshire 03261). The gates allowed each steer access to its own

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feed bunk and thus the collection of individual data on intake. At the south end of the pen, there was a self-filling water tank to which the animals were allowed free access.

Fifteen Santa Gertrudis steers with an average beginning weight of 285 kilograms were used. The animals were dewormed, weighed, and ear-tagged before the start of the experiments. The cattle were fed either baled coastal Bermuda grass (*Cynodon dactylon*) or baled Kleberg bluestem (*Dichanthium annulatum*). Both forages were chopped to a length of three centimeters before feeding to reduce animal waste.

Before the start of the intake trials, in vivo digestion trials were conducted on both forages. Six steers were used in each trial. Seven-day adjustment periods were followed by seven-day periods of data collection. Feces were collected by means of fecal bags, and aliquots of feces and feed were analyzed to determine digestibility (Schneider and Flatt, 1975: table 1).

For the intake trials, five grain rations containing 0, 20, 30, 40, or 50 percent NaCl were prepared for each forage (Table 2). The rations, balanced by the Least Cost Ration Balancing Program at the Texas A&I University Computer Center, were designed to meet the requirements of 273-kilograms, growing-finishing steers gaining 0.45 kilograms per day (NRC 1976). Therefore, the steers required 16.2 Mcal/day digestible energy (DE), 0.34 kg/day digestible protein (DP), and a calcium (Ca) to phosphorus (P) ratio of 1.1:1.

Initial analysis of duplicate samples of the coastal Bermuda grass and Kleberg bluestem hays showed them to contain 8.5 and 4.0 percent crude protein (CP) and 49.3 and 46.0 percent total digestible nutrients (TDN), respectively. The latter values were calculated after chemical determination of neutral detergent fiber (NDF). The computer program balanced the grain rations by estimating the forage intake, subtracting from the steers' requirements the nutrients supplied by forage, and determining the grain mix required to supply the deficient nutrients. To calculate the salt-containing grain mixes, the program substituted salt for a portion of the corn and cottonseed meal (CSM). Protein and energy contents of the grain mixes declined proportionately as the salt content in the mixes increased.

Each of the four intake trials consisted of a 10-day adjustment period followed by a seven-day period of data collection. The 15 steers were randomly divided into five groups of three steers each. During the first two trials, chopped coastal Bermuda grass was offered to all animals ad libitum at 0800 daily. At 1700, feed bunks were cleaned, and hay orts were collected and weighed. The five grain mixes of Ration 1 were offered to the five groups of cattle at 1700 daily, and the grain orts were collected at 0800. The steers were re-randomized at the end of each trial. During the second two trials, chopped Kleberg bluestem was substituted as the forage, as well as the five grain mixes of Ration 2.

The hay, grain, and fecal samples were analyzed for dry matter (DM) according to AOAC (1970) methods. Crude protein was determined by the micro Kjeldahl procedure (AOAC 1970; Hertel, 1975). Acid detergent fiber (ADF), cellulose (CELL), and lignin (LIG) were determined by the procedure outlined by Goering and Van Soest (1970). Sodium (Na) determinations were performed by flame photometry at the Texas Agricultural Extension Service Soil Testing Laboratory, Texas A&M University, College Station (AOAC, 1970). Chloride (Cl) determinations were performed as outlined by Harris (1970). Gross energy was determined using the Parr adiabatic bomb calorimeter (Parr Instrument Company, 1975). The water offered to the cattle was analyzed by flame photometry and found to contain 315 parts per million of Na and 253 of Cl.

A completely randomized two-factor factorial design was employed to investigate differences in the effects of salted grain mixes and forages. The model used was:

$Y_{ijk} = U + S_i + F_j + (SF)^{ij} + E_{ijk}$, where
Y_{ijk} = dependent variable,
U = true overall mean,
i = 1, 2, 3, 4, 5 salt levels,
j = 1, 2 forages, and
k = 1, 2, 3 animals.

TABLE 1. Chemical composition and digestibility of forages.

Feed analysis[1]	Coastal Bermuda grass[2]	DC[3]	Kelberg bluestem[2]	DC[3]
Dry matter, %	93.9	0.52	94.2	0.56
Crude protein, %	5.7	0.51	3.3	0.33
Acid detergent fiber, %	44.8	0.50	57.1	0.55
Cellulose, %	31.7	0.63	37.0	0.67
Lignin, %	7.1	0.36	7.7	0.30
Gross energy, Mcal/kg	4.2	0.53	4.1	0.60
Crude fiber, %	33.0		37.0	
Sodium, %	0.05		0.02	
Chlorine, %	0.53		0.49	

[1] Dry matter basis.

[2] Values are means of six observations of a seven-day collection period.

[3] Digestion coefficient.

The above model was used to analyze the following dependent variables: HDMI . . . Hay intake (DMIg/BW$^{0.75}$kg); GDMI . . . grain intake (DMIg/BW$^{0.75}$kg).

In order to predict GDMI at different levels of salt, two regression equations were generated using GDMI as the dependent variable. In both equations a second term (quadratic) was added on the basis of its ability to provide significantly more predictive power than the single term. To obtain a quantitative measure of how well the second term predicted the dependent variable, the square multiple correlation coefficient (R^2) was obtained. A highly significant improvement ($P < .01$) in the percentage change of R^2 was obtained by the quadratic term. Addition of a third term (cubic) to the equation was not significant ($P > .05$). Duncan's Multiple Range Test was employed to compare means.

RESULTS AND DISCUSSION

Digestibilities of coastal Bermuda grass and Kleberg bluestem when fed alone are presented in Table 1. The digestibility of DM, ADF, CELL, and energy was higher for Kleberg bluestem. The CP digestibility, on the other hand, was higher for coastal Bermuda grass. Thus the quality of the two hays, as measured by their digestible nutrients, was much closer than originally estimated. The digestion coefficient for lignin was found to be 0.36 in coastal Bermuda grass and 0.30 in Kleberg bluestem. This may have been attributed to the procedure used (Potassium permanganate), which may not have accounted for all of the fecal lignin (Wallace and Van Dyne, 1970).

Grain DMI/BW$^{0.75}$ of the salt-free rations was higher ($P < .01$) than that of the salted grain mixes (Table 3). While there was a tendency for grain intake to decline with increasing salt concentrations, the differences in GDMI were not significant between the salted grain mixes. When coastal Bermuda grass was offered as the forage, GDMI was lower at each level of salt than it was for Kleberg bluestem, although not significantly (Table 3). Previous research suggests that the percentage of salt necessary to regulate intake of supplements depends on such factors as age, weight,

TABLE 2. Composition of salted grain rations.[1]

Ingredients	Ration 1[3]				
Salt, %	0.0	20.0	30.0	40.0	50.0
Corn, %	99.0	79.2	69.3	59.4	49.5
Limestone, %	1.0	0.8	0.7	0.6	0.5
Nutrients[2]					
DP, %	7.4	5.9	5.2	4.5	3.7
DE, Mcal/kg	3.9	3.1	2.7	2.3	1.9
Ingredients	Ration 2[4]				
Salt, %	0.0	20.0	30.0	40.0	50.0
Corn, %	82.7	66.2	57.9	49.6	41.4
Cottonseed meal, %	16.0	12.8	11.2	9.6	8.0
Limestone, %	1.3	1.0	0.9	0.8	0.6
Nutrients[2]					
DP, %	12.0	9.6	8.4	7.2	6.0
DE, Mcal/kg	3.8	3.0	2.6	2.3	1.9

[1] Rations balanced to meet NRC (1976) requirements for 273-kg steers gaining 0.46 kg/day.
[2] CP and DE were calculated according to NRC (1976).
[3] Fed to steers receiving coastal Bermuda grass.
[4] Fed to steers receiving Kleberg bluestem.

and type of animal (Riggs et al., 1953). Rich et al. (1976) reported the requirement of salt in cattle to be roughly 28 grams per head per day or 0.1 pound salt per 100 pounds body weight. Fowler (1969), Ensminger (1976), and Newmann (1977) all reported a standard of 25 percent salt in protein rations to restrict intake to two pounds a day. Ensminger (1976) also stated that 33 1/3 percent would result in an intake of 1.5 pounds per day, or "a reduction in salt level of 33 1/3 percent to 24 percent will increase consumption 50 percent."

In order to predict GDMI at predetermined levels of salt, two equations were generated. A regression analysis using GDMI as the dependent variable generated the following equations for coastal Bermuda grass and Kleberg bluestem respectively: 1) $\text{GDMIg/BW}^{0.75}\text{kg} = 0.148 - 0.060\ (\%\ \text{NaCl}) + 0.007\ (\%\ \text{NaCl})^2$, $R^2 = 94.9\%$; 2) $\text{GDMIg/BW}^{0.75}\text{kg} = 0.151 - 0.053\ (\%\ \text{NaCL}) + 0.005\ (\%\ \text{NaCl})^2$, $R^2 = 92.4\%$.

Average dry matter consumption of coastal Bermuda grass per ($\text{BW}^{0.75}\text{kg}$) was significantly higher than the consumption of Kleberg bluestem (Table 3). Coastal Bermuda grass and Kleberg bluestem dry matter consumption (5.95 and 5.20 kilograms per head per day, respectively) was significantly higher when fed alone in the preliminary digestion trials than when grain (salt excluded) was fed in the feeding trials (4.92 and 3.73 kilograms per head per day) (Creixell, 1982).

Coastal Bermuda grass consumption ($\text{kg/BW}^{0.75}\text{kg}$) increased slightly but not significantly until the grain mixture contained 30 percent salt, when hay intake leveled off, then declined with the addition of 50 percent salt

TABLE 3. Consumption of coastal Bermuda grass (CB), Kleberg bluestem (KBS) and salted grain mixes fed ad libitum[1].

		Grain intake		Hay intake		Salt intake	Salt intake	
% NaCl	Forage	DMI/BW$^{0.75}$kg	SE	DMI/BW$^{0.75}$kg	SE	g/head/day	% BW	SE
0	CB	0.68^{a}	0.019	0.73^{a}	0.011	0	0	0
	KBS	0.70^{a}	0.001	0.53^{b}	0.004	0	0	0
20	CB	0.21^{b}	0.007	0.75^{a}	0.003	330	0.230^{a}	.018
	KBS	0.26^{b}	0.020	0.61^{b}	0.009	400	0.277^{a}	.054
30	CB	0.14^{b}	0.003	0.78^{a}	0.001	340	0.228^{a}	.012
	KBS	0.21^{b}	0.005	0.58^{b}	0.007	490	0.343^{a}	.028
40	CB	0.08^{b}	0.002	0.78^{a}	0.005	250	0.183^{ab}	.026
	KBS	0.14^{b}	0.002	0.59^{b}	0.013	400	0.288^{ab}	.027
50	CB	0.06^{b}	0.002	0.66^{a}	0.011	230	0.151^{b}	.016
	KBS	0.07^{b}	0.004	0.61^{b}	0.006	260	0.192^{b}	.023

[1] Values are means of seven-day observations on six steers. Numbers in columns with different superscripts are significantly different ($P < 0.05$).

(Table 3). Kleberg bluestem consumption (kg/BW$^{0.75}$kg) was non significantly higher for all the salt levels than for the zero percent salt-grain mix. Analysis of variance showed the percentage salt did not affect HDMI significantly ($P > .05$) compared with the controls, and that there was no significant interaction ($P > .05$) between the salt levels and the hay quality. Thus, as salt was added to the grain mix, the hay digestible energy (DE) intake (Mcal/day) changed little, whereas the grain DE intake decreased.

Analysis of variance showed no significant interaction between the two forages and five grain mixes in salt intake per unit body weight. (Table 3). Salt intake as a percent of the body weight was greatest at 20 percent (CB) or 30 percent (KBS) salt and least at 50 percent salt in the grain mix for both forages. This decline in salt intake per unit body weight at the 50 percent salt level could signify a palatability problem. The overall salt intake per unit body weight for both forages over all grain mixes was 0.189 percent (±0.016). This finding is in general agreement with Corah (1980), who suggested that cattle have a salt requirement of 0.1 percent of their body weight.

Although the highest salt intake was recorded at the 30 percent level (490 grams), no serious effects were noted in any of the groups of steers fed the grain-salt ration. Scouring, although never serious, occurred in two steers of the salt-fed groups. There was some decline in the condition of the hair and fleshing at the close of the experiments because the nutrient content of the forages and grain was enough only to maintain the steers at a constant weight.

SUMMARY AND CONCLUSIONS

Average daily consumption of coastal Bermuda grass (5.96 kg) and Kleberg bluestem (5.20 kg) when fed alone did not provide adequate levels of DP (0.17 and 0.05 kg) or DE (13.01 and 12.81 Mcal/day) for the steers to meet their requirements. Thus, the addition of supplemental feed was necessary. When supplemental feed was included in the diet, cattle in the control group consumed enough of the hay-grain mix to obtain adequate DE (estimated 28.57 and 27.67 Mcal/day) for the two forages, respectively. These figures, when compared with the requirements of DE (16.20 Mcal/day) indicate, however, that cattle consumed more grain than necessary in the control group. On the other hand, when salt was added to the grain mix, grain intake was restricted such that cattle failed to consume adequate total DE. Because 20 percent salt was the lowest salt level considered in this study, it appears that the level of grain intake needed for a balanced diet when either coastal Bermuda grass or Kleberg bluestem is offered as the forage, would be between 0 and 20 percent salt.

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GENERAL NOTES

CALORIC CONTENT OF AN EXCAVATED FOOD CACHE OF *PEROGNATHUS FLAVESCENS*

Kent M. Reed
*Department of Wildlife and Fisheries Sciences, Texas A&M University,
College Station, Texas, 77843*

The climate of the Great Plains region is unpredictable and, in winter, may include prolonged subzero temperatures. Accordingly, small mammals that occur there, with their high ratio of surface area to body volume, must have mechanisms by which to cope with periods when foraging above ground is disadventageous energetically.

One of the smaller mammals on the central and northern Great Plains (Jones et al., 1983), the plains pocket mouse (*Perognathus flavescens*) is not known to hibernate and does not accumulate body fat to use as a source of energy in winter (Hibbard and Beer, 1960). Instead, it has a propensity to cache seeds within its underground burrows for use in winter.

Several food caches of *P. flavescens* have been examined (Bailey, 1929; Hibbard and Beer, 1960; Reed and Choate, 1986), but none has been subjected to caloric analysis. A food cache of a plains pocket mouse was uncovered on 20 July 1985 (Reed and Choate, 1986), affording the opportunity to obtain preliminary data on energy storage in this species.

Seeds in the food cache were sorted by phena. Samples were homogenized using a CRC micro-mill and weighed to the nearest 0.0001 of a gram using a Mettler analytical balance. Three of the seed types collected (*Croton texensis, Lithosperma incisum*, and unidentified Compositae) were sufficiently numerous to be analyzed separately. The remaining seeds were combined into one sample for analysis.

Because of the high oil content of certain seeds, samples (excepting that consisting of the combined seeds) were not pressed into pellets but were packed loosely in the crucibles for burning. Gross caloric content then was determined using a Parr adiabatic calorimeter standardized with benzoic acid.

The results of the caloric analysis are sumarized in Table 1. All samples, excepting those of *L. incisum*, had energy values greater than 4000 calories per gram. Two seed types, *C. texensis* and unidentified Compositae, had energy values greater than 5800 calories per gram. Caloric content for the samples averaged 5068.3 calories per gram. Gross caloric content for the cache totaled 356,335 calories.

Although no values of basal metabolic rate for *P. flavescens* are available, estimates for a similar-sized, related species (*P. flavus*) were reported by Wolff and Bateman (1978). They found that *P. flavus* (mean body weight, 8.8 grams) consumed from 0.193 to 0.320 grams

Table 1. Weight, caloric content, total calories, and percent biomass of seeds removed from an excavated cache.

	Grams	Calories per gram	Calories	Percent biomass
Croton texensis	47.30	5829.08	275,715.48	67.3
Lithosperma incisum	18.44	3141.90	57,936.64	26.2
Compositeae	1.78	5879.86	10,466.15	2.5
Other	2.79	4378.87	12,217.05	4.0
Total	70.31		356,335.35	100.0

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of food per day per gram body weight (mean caloric value, 4207 calories per gram) at temperatures ranging from 15° to 1°C. This pocket mouse thus consumes 7145 to 11,847 calories per day without entering torpor. Using these values, *P. flavescens* (weight, 7-12 grams according to Jones et al., 1986) would require from 7713 to 12,789 calories per day under similar conditions. At this rate of energy consumption, assuming no period of torpor, the cache would have lasted approximately 35 days. Presumably, the mouse that accumulated the food cache would have added to it throughout summer and into autumn.

Perognathus flavescens is not known to be active above ground in winter (Hibbard and Beer, 1960; Jones et al., 1986), and above-ground activity is thought to be temperature regulated; in Kansas, for example, *P. flavescens* was not found above ground for four months from mid-November to mid-March (Reed and Choate, 1986). Apparently, frequency and duration of torpor in *P. flavus*, are related to temperature and availability of food (Wolff and Bateman, 1978). By reducing its energy requirement by entering torpor periodically, *P. flavescens* could ration its stores and thereby avoid the need for foraging above ground during periods of extremely cold temperatures.

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AN UNUSUAL "WOODRAT NEST"

Walter W. Dalquest and Greg J. Coln
Midwestern State University, Wichita Falls, Texas 76308
and Box 11, Eagle Nest, Creede, Colorado 81130

On 9 February 1986, the junior author discovered a bird's nest composed mostly of the mummified body of an adult woodrat, *Neotoma mexicana.* The site was on a ridge or shoulder a mile south of the summit of Bristol Head Mountain, approximately 9600 feet elevation, 11.5 miles south of Creede, Mineral County, Colorado. The nest was in a tall wax current (*Ribes ccreum* Dougl.) bush, 1.5 meters from the ground, and 6 meters out from the base of a tall (50 meter) cliff. The ground beyond the bush sloped swiftly to a rocky slide area. An active woodrat nest was located less than 100 meters away.

The mummified carcass was well preserved, except that the fur of the head and part of the chest was missing. The body was curled gently. The bird, approximately the size of a junco to judge from the size of the nest cup, had added bits of grass and vegetation above the mummy, and tucked other bits beneath it (Fig. 1). There was no evidence to indicate

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FIGURE 1. Mummified carcass of woodrat utilized as nest by small bird.

that eggs actually were incubated, but vegetation was packed and the nest obviously had been used.

We speculate that in the previous winter an owl had captured and killed the woodrat, but dropped it in flight. The dense bush prevented retrieval and the cold weather at that high elevation prevented attack of the carcass by insects. The woodrat body was freeze-dried by spring, forming a soft platform for the small bird to use for its nest.

We are grateful to Gregory Pogue for identifying the bush and to Dr. Norman Horner for the photograph of the nest.

DISTRIBUTIONAL RECORD OF *LASIURUS SEMINOLUS* (CHIROPTERA: VESPERTILIONIDAE)

THOMAS E. LEE, JR.
Department of Biology, Angelo State University, San Angelo, Texas 76909

In April 1985, Mr. C. Harrison found a Seminole bat, *Lasiurus seminolus*, caught by a wing on a barbed-wire fence, 6 mi. N Clay, Burleson Co., Texas. The area where the bat was found consists mainly of a large cotton field with oak-hickory forest (sometimes favored by *L. seminolus*) located nearby. This specimen (ASNHC 1984) represents the first record of this species taken west of the Brazos River (Schmidly, 1983; although see Hall, 1981, for discussion of an extralimital specimen taken near Brownsville, Cameron Co., Texas) and extends the known distribution of the Seminole bat approximately 32 kilometers to the west.

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The Texas Journal of Science, Vol. 39, No. 2, May, 1987

NOTOMMATA ALLANTOIS IN NORTHEASTERN TEXAS LAKES: A ROTIFER PREVIOUSLY KNOWN ONLY FROM EUROPE

John Shoemaker, Sally H. Davis, and Robert K. Williams
Department of Biological Sciences, East Texas State University, Commerce, Texas 75428

A comprehensive study of rotifers in Lake Fork, Wood Co., Texas, has been conducted since the autumn of 1982. Lake Fork is a water-supply and recreational lake administered by the Sabine River Authority and covers nearly 28,000 acres (about 11,330 hectares). The reservoir drains a watershed of sandy pastures, dairies, farms, and oak forests. During the study period from autumn 1982 to summer 1985, the pH of the water averaged 6.9 from measurements made by the authors. Occasional algae blooms resulted in slightly alkaline measurements. Specimens of the rare rotifer, *Ptygura elsteri* Koste, 1972, were collected from this lake in October and November, 1984, and in January and March, 1985 (Shoemaker and Williams, 1986). The authors have identified 157 species of rotifers from Lake Fork collections during these studies.

Specimens, which were identified to the genus *Notommata* Ehrenberg, 1830, were found in samples collected on 26 November 1984, 5 March 1985, and 12 March 1985. The species could not be determined by use of keys, illustrations, or descriptions of several authors (Harring and Myers, 1922; Taft, 1932; Edmondson, 1959; Stemberger, 1979; and others). The organism varied greatly from *N. silpha* (Gosse, 1887) and *N. aurita* (Müller, 1786), which had been identified previously from Lake Fork collections.

A striking feature of the organism was a broad posterior projection of the body wall forming a dorsal covering or hood over the proximal segments of the foot, with only the terminal segment and toes projecting beyond the hood (Fig. 1). The organism resembled *N. collaris* Ehrenberg, 1832, and *N. pachyura* (Gosse, 1886) in this regard. These two species (Fig. 1) have the posterior projection of the body wall but neither is as wide as the Lake Fork specimen and *N. collaris* has a shorter covering. In general appearance, the Lake Fork specimens were more rounded and broad of body than either *N. pachyura* or *N. collaris*.

The formula key to the *Notommata* in Voigt and Koste (1978) was used to identify the Lake Fork specimens as members of the *collaris-pachyura-allantois* association (=formenkreis). Use of the key to this association led to the conclusion that the Lake Fork specimens were members of *N. allantois* Wulfert, 1935. According to the formula key and description of Voigt and Koste (1978) the anal appendage is wide, ligulate, and without a

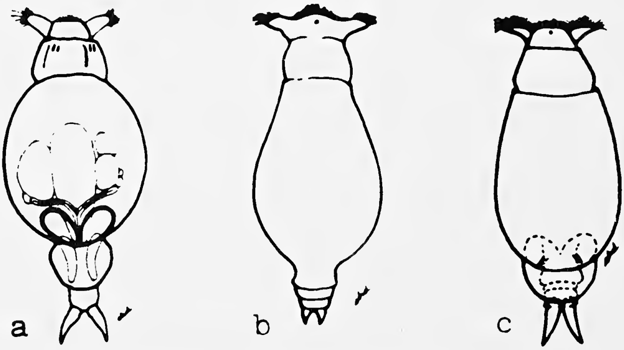

FIGURE 1. The *collaris-pachyura-allantois* association of *Notommata*. Dorsal: a, *N. allantois* (from Lake Fork, Wood Co.; Texas); b, *N. collaris* (redrawn from Voigt and Koste, 1978); c, *N. pachyura* (from Lake Wright Patman, Bowie Co., Texas).

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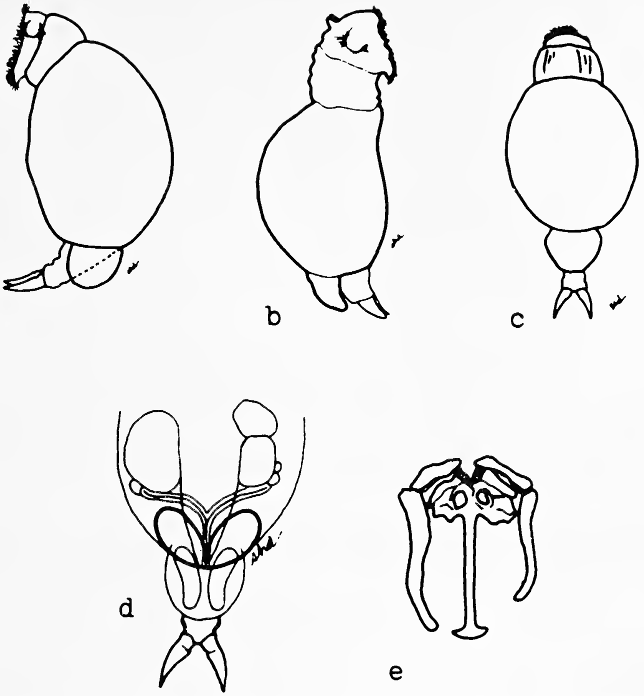

FIGURE 2. *Notommata allantois* from Lake Fork, Wood Co., Texas, profiles and structures: a, lateral, foot extended; b, foot withdrawn; c, dorsal, corona partially withdrawn; d, posterior structures showing bilobed vesicle; e, asymmetrical trophi.

posterior projecting appendage. There is no caudal process on the foot. The toes are greater than 40 micrometers in length and are pointed. The corona auricles are large and ciliated. There is an asymmetrical trophi, the retrocerebral sac extends above the posterior third of the body, and the bladder is two-parted (Fig. 2).

Specific differences among *N. allantois, N. collaris,* and *N. pachyura* are found in the foot and toes (Fig. 1). In *N. allantois*, the toes are pointed, greater than 40 micrometers in length, project outward, and are not segmented. There is no projection on the terminal foot segment. In *N. collaris*, the toes are less than 35 micrometers, conical, and straight. In *N. pachyura*, the toes ae greater than 40 micrometers, pointed, and appear to be two-segmented. There are spurs on the last joint of the foot.

Since the collection of *N. allantois* in Lake Fork in 1984 and 1985, specimens also have been found in abundance in collections from Lake O' the Pines in Harrison Co., Texas, made in November 1985. Voigt and Koste (1978) stated that *N. allantois* was known only from Europe. With the discovery of this organism in Lake Fork and Lake O' the Pines, we believe the distribution of this rotifer is poorly known only because of the lack of extensive studies in North America, other than in the Great Lakes region, and elsewhere. Edmondson (personal communication from W. T. Edmondson, Department of Zoology, University of Washington, Seattle, March, 1985) stated that due to the cosmopolitan nature of rotiferans, it would be expected that such intercontinental range extensions as this would occur as more investigations were conducted.

This research was partially supported by an East Texas State University Faculty Research Grant for the illustrations by Sally H. Davis.

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TWO NOTEWORTHY POPULATIONS OF THE FIDDLER CRAB, *UCA SUBCYLINDRICA*, IN SOUTHERN TEXAS

RAYMOND W. NECK
Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744

At least seven species of fiddler crabs (Ocypodidae: *Uca*) are known from Texas; most populations are found in restricted habitats of the interidal and supratidal portions of coastal areas (Powers, 1977). One species of fiddler crab, *Uca subcylindrica* (Stimpson, 1859), is endemic to hypersaline, brackish, and even quasi-freshwater habitats of semiarid portions of southern Texas and northeastern Mexico (Hildebrand, 1958; Barnwell and Thurman, 1984; Thurman, 1984). This species is known as the puffed fiddler crab (Bright and Hogue, 1972).

Uca subcylindrica is able to exist in a wide variety of habitats over a large part of southern Texas because of highly adaptable physiological capabilities. *U. subcylindrica* is able to withstand greater loss of body water than other species of *Uca* (Rabalais and Cameron, 1985a). Habitats with salinities above 90 parts per thousand can be successfully occupied by this species (Thurman, 1984; Rabalais and Cameron, 1985a). Larval development in *U. subcylindrica* is quite abbreviated and may require only eight days (Rabalais and Cameron, 1983); a typical nursery area is a temporary rain puddle (Rabalais and Cameron, 1983; 1985b). Despite the existence of a highly adaptable physiology, *U. subcylindrica* appears to be an inferior competitor against other *Uca* because multi-species fiddler crab communities generally do not contain *U. subcylindrica* (Thurman, 1984).

Field work in southern Texas has revealed an inland locality for *U. subcylindrica* that is farther from tidal habitats than any other previously reported. Additionally, a human-made pond created in the early twentieth century has become sufficiently saline to support a population of the species.

On 30 March 1981, I collected several adult *U. subcylindrica* in Brooks County, nine kilometers east-southeast of Falfurrias. Collection site was the FM 2191 crossing of Los Olmos Creek, which is a saline marsh dominated by sacahuiste (*Spartina spartinae*). This general area is characterized by high levels of gypsum associated with the Gyp Hill Salt Dome; water was clear brown. This locality is approximately 25 kilometers west of the previously reported westernmost locality (site V on Los Olmos Creek in Thurman, 1984). Wetland areas are not continuous along the bed of intermittent Los Olmos Creek, but distances between neighboring wetland areas evidently can be traversed by the crab during moist periods.

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On 25 September 1980, I collected a series of *U. subcylindrica* from a saline pond in Cameron County, 14 kilometers northwest of Brownsville. This pool, which is located just east of the eastern boundary of Resaca de la Palma State Park, was created in the early twentieth century. A portion of a bend in a resaca (abandoned channel of the Rio Grande) was separated from the rest of the resaca by an eathern dike. Aerial photographs taken on November 1938 revealed an established brush line on this dike that was probably constructed during the 1920's during peak agricultural development of the Lower Rio Grande Valley (Foscue, 1934). Following the creation of this two-hectare pond, runoff accumulation and subsequent evaporation have slowly produced a saline environment. Salinity levels obviously vary with water volume but are sufficiently low to allow growth of water milfoil (*Myriophyllum* sp.). The dominant terrestrial plant is sea ox-eye daisy (*Borrichia frutescens*). Dispersal from naturally occurring saline areas (within 10 kilometers of Resaca de la Palma site) probably occurs during periods of high water level and high ambient relative humidity.

The ability of *U. subcylindrica* to maintain populations in non tidal habitats far from coastal areas and to colonize newly-created saline habitats (also nontidal) results from an adaptable complement of physiological processes. This adaptability has allowed *U. subcylindrica* to invade more terrestrial habitats than other speices of the generally semiterrestrial genus *Uca*.

I thank Nancy N. Rabalais for verification of identify of specimens. Specimens have been deposited in the Texas Memorial Museum.

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A RECORD OF THE WESTERN SMALL-FOOTED MYOTIS, *MYOTIS CILIOLABRUM* MERRIAM, FROM THE TEXAS PANHANDLE

Robert R. Hollander and J. Knox Jones, Jr.
The Museum and Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409

Although reported from the Wichita Mountains and Black Mesa of Oklahoma (Hall, 1981), the western small-footed myotis, *Myotis ciliolabrum ciliolabrum* Merriam, 1886, has been known previously in Texas only from the western counties of the Trans-Pecos region (Davis, 1974; Schmidly, 1977). A record from the Panhandle of that state is, therefore, noteworthy.

On 30 January 1960, the late Donald R. Tinkle and a field party collected hibernating bats in a sinkhole on the Hedgecoke Ranch, 29 mi. SSW Claude, Armstrong Co., Texas. Among the specimens taken was a single *M. c. ciliolabrum*, a skin alone of unrecorded sex (TTU 120), that was orignially misidentified as a pipistrelle (see also Mollhagen, 1973). The golden brown dorsal color, narrow and pointed tragus (5 mm long), small feet, and blackish ears, however, leave no doubt as to the identity of the bat. External measurements (mm) recorded by the preparator are: total length, 77; length of tail, 33; length of hind foot, 6; length of ear, 13. The forearm measures 32.5. We follow Jones et al. (1986) in use of the specific name *ciliolabrum* for this bat in Texas.

Myotis ciliolabrum is a saxicolous species. It is likely, therefore, that individuals hibernate from time to time in the many caves and sinkholes in the Panhandle region and occur there in summer in suitable rocky habitats.

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The Texas Journal of Science, Vol. 39, No. 2, May, 1987

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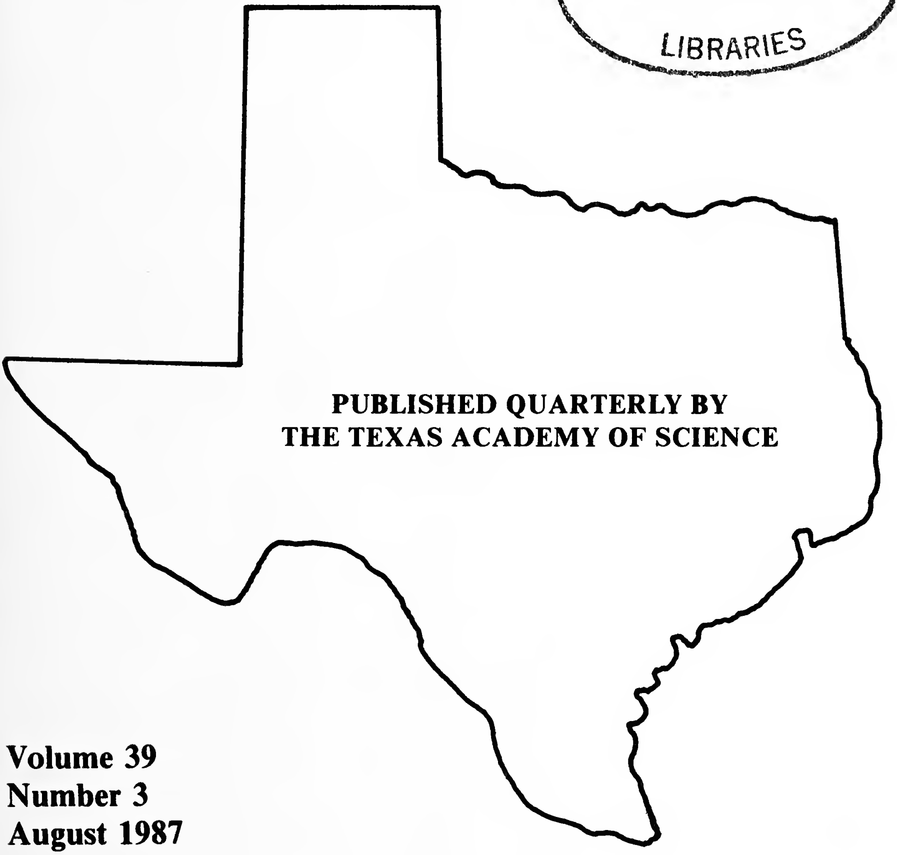

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A FRAMEWORK FOR PLANT COMMUNITY CLASSIFICATION AND CONSERVATION IN TEXAS

DAVID D. DIAMOND, DAVID H. RISKIND, AND STEVE L. ORZELL
Texas Natural Heritage Program, General Land Office, Stephen F. Austin Building, Austin, Texas 78701, and Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744 (DHR)

ABSTRACT.—Seventy-eight late seral stage plant community types are described and classified at the series level (characterized by dominant species or genera). The classification framework used can be expanded to include finer subdivisions at the plant association (defined as a plant community of definite floristic composition within a uniform habitat) level. Community types are ranked according to conservation needs from endangered (1) to secure (4), and 10 (13 percent) are threatened or endangered. Ranking remains partially subjective, but depends on the estimated number of late seral stage relicts, the estimated number of relicts protected, the estimated area occupied by the community type, and the relative threat of severe disturbance. The classification and conservation rankings presented should stimulate debate among users and result in successive refinements. Quantitative data on vegetation are inadequate to provide a finer scale classification of communities for most regions of Texas, and quantitative inventories of resources already in public or private managed natural areas also are lacking. The need for these data, the need for enlightened stewardship of existing natural areas, and the need to consider landscape ecology in preserve design and selection mark the greatest challenges in the future for Texas conservationists. *Key words*: classification; conservation; landscape ecology; plant community.

The land area of Texas is more than 370,000 square kilometers. Climatic regimes range from humid subtropical to arid subtropical to continental steppe (Larkin and Bomar, 1983; Owen and Schmidly, 1986), while geologic substrate ranges from Recent sands and silts to Cretaceous limestones to Precambrian granite (Sellards et al., 1966). This wide variation in climate and geology results in a wide variation in landform, soils, and vegetation. Soils have been classified and mapped to a relatively fine degree across most of Texas. However, there has been no attempt at a fine-scale, state-wide classification of vegetation, although several authors have classified the vegetation at a physiognomic or natural region level (see Tharp, 1939; Gould, 1975; Küchler, 1964; LBJ School of Public Affairs, 1978; Brown et al., 1979; Fig. 1).

An informal approach to classification has generally been adopted by North American ecologists, who have used different approaches and frameworks for different vegetation types and purposes. However, there is merit in acceptance of a standardized classification, because this favors more efficient organization and communication of information among users (see Driscoll et al., 1984). Because conservation efforts generally concentrate on late seral stage, rather than early or mid-successional

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FIGURE 1. The natural regions of Texas (after LBJ School of Public Affairs, 1978).

communities, a standardized classification of such communities is appropriate for present purposes.

History suggests that conservation efforts often overlook the most rare and endangered community types (Gehlbach, 1975). The result of well-meaning but poorly informed and directed protection efforts is often the preservation of numerous examples of relatively common and secure types, usually because they are the most easily acquired or the most aesthetically appealing. A well-founded classification of community types, together with ranks that are based on the rarity and need for protection of each type, should help direct conservation efforts.

Awareness of the need for conservation recently has increased in Texas. The Texas Natural Heritage Program was established within the General Land Office in 1983 to provide a biological inventory of rare species and habitats. A Resource Protection Division was legislatively mandated and established within the Texas Parks and Wildlife Department in 1985. The Texas Organization for Endangered Species established a community protection committee in 1986. Despite growing public awareness, however, surprisingly little is known about the status of plant community protection in Texas (Gehlbach, 1975; Carls and Ludeke, 1984). The purpose of this review is to provide a classification of communities, plus propose conservation ranks for community types and forward suggestions on the direction of future conservation efforts in Texas.

CLASSIFICATION FRAMEWORK

The classification framework used is modified from Driscoll et al. (1984), who, in turn, used a framework provided by UNESCO (1973). A similar framework has been applied in other regions (see Brown et al., 1979; Paysen et al., 1980; Buck and Paysen, 1984). The top level of this hierarchial framework is the class, which is based on dominant growth form. These are:

1. Forest—communities formed by trees at least three meters tall, with a canopy of 61 percent or more.
2. Woodland—communities dominated by trees with 26 to 60 percent canopy (this includes "open forest" and "savannah" types of some authors).
3. Shrubland—communities composed of shrubs from half a meter to three meters tall with 26 percent or more canopy cover.
4. Dwarf Shrubland—communities with 26 percent or more canopy cover of shrubs less than half a meter tall (this category includes heathlands and shrub-dominated wetlands—none are described for Texas).
5. Herbaceous Vegetation—communities dominated by grasses, graminoids, or forbs with less than 25 percent canopy cover of woody plants.

Two additional classes associated with aquatic regimes are recognized here, but were not described by Driscoll et al. (1984):

6. Swamps—forested or shrub-dominated wetlands, with standing water at the surface at least 50 percent of the year and hydric soils.
7. Marshes—herbaceous-dominated wetlands, with standing water at least 50 percent of the year and hydric soils.

The next level in the hierarchy is the subclass. Nineteen subclasses are recognized based on morphological characteristics of dominant species, such as evergreen or deciduous habit or adaptation to temperature and water.

Two levels of hierarchy below the subclass, the group and formation, will not be adopted here. They are based on different criteria for different vegetation types, and there is often difficulty is assigning lower level taxa (series or associations, described below) to formations or groups. Assignment of lower level taxa to groups or formations would provide little additional understanding of their interrelationships, and might even cause confusion.

The lowest levels in the hierarchy are the series and the association. Series are characterized by specificity of structure and physiognomy of the vegetation (Mueggler and Stewart, 1980; Pfister and Arno, 1980). They are named for typical dominant or co-dominant species or, in a few cases, genera. Series are defined to allow for some differences in species composition and dominance relationships among representitive stands, and thus local variants are circumscribed. Associations, subdivisions of series, are plant community types of definite floristic composition within a uniform habitat. They are named and recognized by dominant or co-dominant species. Associations have been quantatively defined for parts of Texas, but are unknown across most of the state. Hence for uniformity's sake, vegetation is classified only to the series level in the following sections. The term "community type" is applied to both series and associations.

CLASSIFICATION OF LATE SERAL VEGETATION

Forest and Woodland

Fourteen forest and 19 woodland community types were defined (Table 1). Forests of both uplands and floodplains of the East Texas Piney Woods are relatively well known (Tharp, 1926; Nixon et al., 1973; Chambless and Nixon, 1975; Nixon and Raines, 1976; Nixon et al., 1977; Watson; 1979; Nixon et al., 1980; Hinton, 1981; Marks and Harcombe, 1981; Marietta and Nixon, 1983; Nixon et al., 1983), and 10 community types are defined. The sweetbay (*Magnolia virginiana*) series is among the most broadly defined of these, and may range from mainly deciduous forest in the north to mainly evergreen shrubland ("baygalls") in the south. Vegetation of the Post Oak Savannah and Cross Timbers to the west is not as well known, and one forest and one woodland series is indicated based on data from McBryde (1933), Dyksterhuis (1948), McCaleb (1954), Rice and Penfound (1959), Risser and Rice (1971), Marcy (1982), Marietta and Nixon (1983), Ward (1983), and others. Two coastal live oak (*Quercus virginiana*) co-dominated woodlands are indicated within the Coastal Prairie. These are for the most part restricted to the Upper Coastal Prairie, with the coastal live oak-post oak (*Quercus virginiana-Quercus stellata*) usually over clay pan soils with a loamy surface layer and the coastal live oak-pecan (*Quercus virginiana-Carya illinoensis*) usually over clayey soils. The coastal live oak-seacoast bluestem (*Quercus virginiana-Schizachyrium scoparium* var. *littoralis*) series inhabits sandy soils of the Coastal Sand Plains. Subtropical vegetation of the lower Rio Grande Valley is likewise not well known, but one forest and one woodland series is defined based on field surveys and data from Clover (1933), Davis (1942), Everitt and Gonzales (unpublished data) and Neck et al. (unpublished data). Four woodland community types of the Edwards Plateau, Balcones Canyonlands, and Llano Uplift are defined by data from Beuchner (1944), Tolstead and Cory (1946), Van Auken et al. (1978, 1979, 1981), Ford and Van Auken (1982), Van Auken and Bush (1985), Gehlbach (1988), Riskind and Diamond (1988), and others.

Riparian forests and woodlands west of the Piney Woods are poorly known, but often contain some combination of sugarberry (*Celtis laevigata*), hackberry (*Celtis reticulata*), elm (*Ulmus* sp.), ash (*Fraxinus* sp.), oaks (*Quercus* sp.), and pecan among the dominants. Hence, a sugarberry-elm series is indicated. Likewise, water and coastal live oaks are often among the dominants of Upper Coastal Prairie floodplains, and a water oak-coastal live oak series is designated. Additional data on these community types are in Beuchner (1944), Nixon (1975), Allen (1974), Ford and Van Auken (1982), Mohler (1979), Van Auken and Bush (1985), Gehlbach (1988), and Riskind and Diamond (1988).

Deciduous riparian woodlands of the Trans-Pecos generally contain some combination of ash, willow (*Salix* sp.), cottonwood (*Populus* sp.), hackberry, and walnut (*Juglans* sp.) as dominants. The three series defined are based primarily on data from Webster (1950), Gehlbach (1967), Burgess and Northington (1974), Johnston (1974), Riskind (1976), and Brown et al. (1979). Four series dominated by pine (*Pinus* sp.), juniper (*Juniperus* sp.) or oak are described for the Trans-Pecos mountains, and are based on data from Gehlbach (1967), Brown et al. (1979), and Johnston and Henrickson (1987).

Shrubland

Shrublands dominate the contemporary landscape of the South Texas Plains and Trans-Pecos (Table 2). Desert shrublands and deciduous shrublands of the Trans-Pecos are relatively well known, and 10 series are indicated based on data from Webster (1950), Burgess and Northington (1974), Johnston (1974), Brown (1982), Burgess and Klein (unpublished data), Johnston and Henrickson (1987), and others. In contrast, composition of late seral stage shrublands of the South Texas Plains is poorly known. The four series listed are based primarily on field surveys and data from Clover (1933), Johnston (1952), Davis and Speicer (1965), Fanning et al. (1965), Drawe et al. (1979b), Everitt and Gonzales (unpublished data), Lonard et al. (1987), and Neck and Riskind (unpublished data).

Communities dominated by Havard shin oak (*Quercus havardii*) and tall grasses inhabit stabilized dunes in the High Plains, northern Rolling Plains, and northeastern Trans-Pecos. Slightly finer textured sandy soils, or disturbed sites, have sandsage (*Artemisia filifolia*) and mid-grasses. These are described as belonging to a Havard shin oak-tallgrass or sand sage-midgrass series. Over thin limestone soils in the High Plains and Rolling Plains, especially slopes of the Red River Valley, Mohr's shin oak (*Quercus mohriana*) is often dominant, and hence a Mohr's shin oak series is defined. Additional information is found in Johnston (1974), Warnock (1974), Eyre (1980), McMahan et al. (1984), and unpublished data from the U. S. Soil Conservation Service.

The redberry juniper-midgrass (*Juniperus pinchotii*) and one seed juniper-midgrass (*J. monosperma*) series inhabit the Rolling Plains and High Plains, with juniper-dominated shrubland especially common over caliche or shallow soils. The former also occurs on the Stockton Plateau and Trans-Pecos Mountains, along with the scrub oak-mountain mahogany (*Quercus pungens—Cercocarpus montanus*) series. There is variation with exposure and substrate, and a number of different shrub and grass species are associated with different species of juniper (Webster, 1950; Warnock, 1970; Adams, 1979; unpublished data, U. S. Soil Conservation Service).

TABLE 1.—Late seral stage forest (dominants are trees more than three meters tall, forming 61 percent or more canopy) and woodland (dominants are trees forming 26-60 percent canopy) community types of Texas, with conservation ranks (1, endangered; 2, threatened; 3, apparently secure; 4, secure). Evergreen and deciduous forests are followed by evergreen and deciduous woodlands. Primary region of occurrence after LBJ School of Public Affairs (1978).

Community type	Primary region of occurrence	Conservation rank
Mainly Evergreen Forest		
Douglas Fir-Pine Series (*Pseudotsuga menziesii-Pinus* sp.)	11a	4
Ponderosa Pine Series (*Pinus ponderosa*)	11a	4
Texas Palmetto Series (*Sabal texana*)	6c	1
Mainly Deciduous Forest		
American Beech-Southern Magnolia Series (*Fagus grandifolia-Magnolia grandiflora*)	1a	2
Baldycypress-Sycamore Series (*Taxodium distichum-Platanus occidentalis*)	7b	3
Loblolly Pine-Oak Series (*Pinus taeda-Quercus* sp.)	1b, 1a	4
Overcup Oak Series (*Quercus lyrata*)	1a, 1b, 2a, 3a	3
Post Oak-Black Hickory Series (*Quercus stellata-Carya texana*)	2a, 2b, 3a	3
Shortleaf Pine-Oak Series (*Pinus echinata-Quercus* sp.)	1b	4
Sugarberry-Elm Series (*Celtis laevigata/C. reticulata-Ulmus* sp.)	2, 3, 4, 6, 7 8, 9	3
Swamp Chestnut Oak-Willow Oak Series (*Quercus michauxii-Q. phellos*)	1a, 1b	3
Sweetbay Series (*Magnolia virginiana*)	1a, 1b	3
Water Oak-Sweetgum Series (*Quercus nigra-Liquidambar styraciflua*)	1a, 1b	3
Water Oak-Coastal Live Oak Series (*Quercus nigra-Q. virginiana*)	4c	3
Mainly Evergreen Woodland		
Ashe Juniper-Oak Series (*Juniperus ashei-Quercus* sp.)	7a, 7b	4
Coastal Live Oak-Seacoast Bluestem Series (*Quercus virginiana-Schizachyrium soparium* var. *littoralis*)	5	3
Longleaf Pine-Rhynchospora Series (*Pinus palustris-Rhynchospora* sp.)	1a	3
Longleaf Pine-Tallgrass Series (*Pinus palustris*)	1a	2
Pinyon Pine-Oak-Juniper Series (*Pinus cembroides/P. edulis-Quercus* sp.-*Juniperus sp.*)	11a	4

TABLE 1.—Continued.

Rocky Mountain Juniper Series *(Juniperus scopulorum)*	9b, 10	4
Texas Ebony-Anacua Series (*Pithecellobium flexicaule-Ehretia anacua*)	6c	1
Mainly Deciduous Woodland		
Bluejack Oak-Pine Series (*Quercus incana-Pinus* sp.)	1a, 1b, 2a	3
Coastal Live Oak-Pecan Series (*Quercus virginiana-Carya illinoensis*)	4c	3
Coastal Live Oak-Post Oak Series (*Quercus virginiana-Q. stellata*)	4c	3
Freemont Cottonwood-Willow Series (*Populus freemontii-Salix* sp.)	11a, 11b, 11c, 11f	3
Gray Oak-Oak Series (*Quercus grisea-Quercus* sp.)	11a, 11b, 11f	4
Lacey Oak Series (*Quercus glaucoides*)	7a, 7b	3
Mesquite-Huisache Series (*Prosopis glandulosa-Acacia farnesiana*)	4c, 6a, 11c, 11f	4
Netleaf Hackberry-Little Walnut Series (*Celtis reticulata-Juglans microcarpa*)	11b, 11c, 11f	3
Pine-Bluejack Oak Series (*Pinus* sp.-*Quercus incana*)	1a, 1b	3
Plateau Live Oak Series (*Quercus fusiformis*)	7a, 8	3
Post Oak-Blackjack Oak Series (*Quercus stellata-Q. marilandica*)	2a, 2b, 2c	4
Texas Oak Series (*Quercus texana*)	7b, 7c	3
Velvet Ash-Willow Series (*Fraxinus velutina-Salix* sp.)	11a, 11b, 11c	3

Herb-Dominated Communities

Seventeen herb-dominated community types were identified (Table 3). Six are tallgrass communities, with four inhabiting the Blackland, Fayette, and Upper Coastal prairies. They are described based on data from Dyksterhuis (1946), Launchbaugh (1955), Diamond (1980, 1983), Dunlap (1983), and Diamond and Smeins (1984, 1985). The seacoast bluestem series often contains gulfdune paspalum (*Paspalum monostachyum*) and sedges, and inhabits stabilized dunes and flats of the barrier islands, plus the Coastal Sand Plains. It is defined on data from Johnston (1955, 1963) and Judd et al. (1977). The cenicella-beach morning glory (*Sesuvium portulacastrum-Ipomoea stolonifora*) series occurs on partially stabilized coastward barrier island dunes, and is defined primarily on data from Chabreck (1972), Judd et al. (1977), Drawe et al. (1979a), and Lonard and Judd (1980).

TABLE 2.—Late seral stage shrublands (dominants are shrubs or small trees half a meter to three meters tall, forming 26 percent or more canopy) of Texas, with conservation ranks (1, endangered; 2, threatened; 3, apparently secure; 4, secure). Evergreen shrublands are followed by deciduous shrublands and xeromorphic shrublands. Primary region of occurrence after LBJ School of Public Affairs (1978).

Community type	Primary region of occurrence	Conservation rank
Mainly Evergreen Shrubland		
Ceniza series (*Leucophyllum frutescens*)	6a	3
Havard Shin Oak-Tallgrass Series (*Quercus havardii*)	9, 10, 11e	3
Oneseed Juniper-Midgrass Series (*Juniperus monosperma*)	9a, 9b, 10	4
Redberry Juniper-Midgrass Series (*Juniperus pinchotii*)	9a, 9b, 10, 11a, 11f	4
Sandsage-Midgrass Series (*Artemisia filifolia*)	9a, 10	4
Scrub Oak-Mountain Mahogany Series (*Quercus pungens-Cercocarpus montanus*)	11a, 11b	4
Mainly Deciduous Shrubland		
Apache-plume Series (*Fallugia paradoxa*)	11b, 11c, 11f	4
Blackbrush Series (*Acacia rigidula*)	6a	4
Fern Acacia Series (*Acacia berlandieri*)	6a, 6b, 11f	4
Mesquite-Sandsage Series (*Prosopis glandulosa-Artemisia filifolia*)	11b, 11c, 11e, 11f	4
Mohr's Shin Oak Series (*Quercus mohriana*)	9a, 9b, 7a, 11f	4
Rough Tequilia Series (*Tequilia hispidissima*)	11c, 11d	3
Texas Ebony-Snake-eyes Series (*Pithecellobium flexicaule-Phaulothmnus spinescens*)	6c	2
Xeromorphic (Desert) Shrubland		
Creosotebush-Mariola Series (*Larrea tridentata-Parthenium incanum*)	11b, 11c	4
Creosotebush-Tarbush Series (*Larrea tridentata-Florensia cernua*)	11c	4
Giant Dagger Series (*Yucca faxoniana*)	11a, 11c	4
Lechuguilla-Sotol Series (*Agave lecheguilla-Dasylirion leiophyllum*)	11b, 11c	4
Mesquite-Saltbush Series (*Prosopis glandulosa-Atriplex* sp.)	11c	4
Whitethorn Acacia Series (*Acacia neovernicosa*)	11a, 11c	4

TABLE 3.—Herb-dominated (dominants are herbaceous, with less than 26 percent canopy of woody species) community types of Texas, with conservation ranks (1, endangered; 2, threatened; 3, apparently secure; 4, secure). Tall grasslands are followed by medium tall and short grassland and herbaceous community types. Primary region of occurrence after LBJ School of Public Affairs (1978).

Community type	Primary region of occurrence	Conservation rank
Tall Grassland (dominants more than 1 meter)		
Gammagrass-Switchgrass Series (*Tripsacum dactyloides-Panicum virgatum*)	3a, 4c	1
Little Bluestem-Brownseed Paspalum Series (*Schizachyrium scoparium-Paspalum plicatulum*)	4c	2
Little Bluestem-Indiangrass Series (*Schizachyrium scoparium-Sorghastrum nutans*)	3a, 4c	1
Cottonwood-Tallgrass Series (*Populus deltoides*)	9a, 10	2
Silveanus Dropseed Series (*Sporobolus silveanus*)	3a	2
Seacoast Bluestem Series (*Schizachyrium scoparium* var. *littoralis*)	4a, 5	3
Medium Tall Grassland (dominants 0.5-1.0 meter)		
Alkali Sacaton-Fourwing Saltbush Series (*Sporobolus airoides-Atriplex canescens*)	11c, 11d, 11e, 11f	3
Black Grama-Sideoats Grama Series (*Bouteloua eriopoda-B. curtipendula*)	11a, 11b	3
Cane Bluestem-Mesquite Series (*Bothriochloa barbinodis-Prosopis glandulosa*)	6a	3
Curlymesquite-Sideoats Grama Series (*Hilaria belangeri-Bouteloua curtipendula*)	7a	3
Little Bluestem-Sideoats Grama Series (*Schizachyrium scoparium-Bouteloua curtipendula*)	9a	3
New Mexico Little Bluestem-Wolftail Series (*Schizachyrium scoparium* var. *neomexicana-Lycurus phleoides*)	11a	3
Sideoats Grama-Mesquite Series (*Bouteloua curtipendula-Prosopis glandulosa*)	9a, 10	3
Short Grassland (dominants less than 0.5 meter)		
Blue Grama-Buffalograss Series (*Bouteloa gracilis-Buchloe dactyloides*)	7a, 10	4
Tobosa Series (*Hilaria mutica*)	7a, 10, 11b, 11c	3
Forb-Dominated Vegetation		
Cenicilla-Beach Morning Glory Series (*Sesuvium portulacastrum-Ipomoea stolonifera*)	4a	4
Bogs		
Sphagnum-Rhynchospora Series (*Sphagnum* sp.-*Rhynchospora* sp.)	1a, 2a	3

The cottonwood-tallgrass (*Populus deltoides*) series of the Rolling Plains and High Plains has been little studied, but because of unique species composition probably warrants recognition as a separate community type (Bruner, 1931; Tolstead and Cory, 1946; Allred, 1956; unpublished data, U. S. Soil Conservation Service). Likewise, the sphagnum-rhynchospora (*Sphagnum* sp.-*Rhynchospora* sp.) series, found primarily in eastern Texas, denotes bogs that have not been intensively studied, but general descriptions can be found in Rowell (1949), Penfound (1952), Ajilvsgi (1979), Watson (1979), and Nixon and Ward (1986).

The seven midgrass and two shortgrass community types are mainly confined to central and western Texas. They often are intermixed with shrublands, with shrubs being more prevalent in the contemporary landscape. Descriptions are based on Beuchner (1944), Dyksterhuis (1948), Webster (1950), Allred (1956), Brown and Schuster (1969), Smeins et al. (1976), Brown (1982), Dunlap (1983), Fowler and Dunlap (1986), Riskind and Diamond (1988), and unpublished data from the U. S. Soil Conservation Service.

Swamps and Marshes

Within eastern Texas, one forested and two shrub-dominated swamps are defined (Table 4) based on data from Ajilvsgi (1979), Watson (1979), Marks and Harcombe (1981), and Nixon and Ward (1986). A black mangrove (*Avicennia germinans*) series is indicated for the South Texas coast based on descriptions from Clover (1933), McMillan (1971), and Lonard et al. (1987). Black mangroves are well established only along the far South Texas coast, and even there they are subject to periodic diebacks due to freezing temperatures (McMillan, 1971). The five marsh series defined generally correspond to differences in salinity, with the saltgrass (*Distichlis spicata*), gulf cordgrass (*Spartina spartinae*), and rush-sedge (*Juncus* sp.) series occurring inland as well as along the coast, and the rest confined to coastal areas. Descriptions can be found in Chabreck (1972), Judd et al. (1977), Drawe et al. (1979a), and Lonard and Judd (1980).

CONSERVATION RANKS

Community types were ranked according to conservation priorities by considering the following criteria, range-wide: (1) estimated number of late seral stage relicts—A=0-5, B=6-20, C=21-100, D=more than 100; (2) relative threat of severe disturbance—A=extreme, B=moderate, C=probably none, D=none; (3) estimated number of protected relicts—A=0-1, B=2-5, C=6-10, D=more than 10; and (4) estimated area occupied by the community type, or seral stages of the community type

TABLE 4.—Swamp (wetlands with woody dominants) and marsh (wetlands with herbaceous dominants) community types of Texas, with conservation ranks (1, endangered; 2, threatened; 3, apparently secure; 4, secure). Primary region of occurrence after LBJ School of Public Affairs (1978).

Community type	Primary region of occurrence	Conservation rank
Swamps		
Black Mangrove Series (*Avicennia germinans*)	6c	4
Baldcypress Series (*Taxodium distichum*)	1a, 1b	3
Buttonbush Series (*Cephalanthus occidentalis*)	1a, 1b, 4c	4
Water Elm-Swamp Privet Series (*Planera aquatica-Forestiera acuminata*)	1a, 1b	4
Marshes		
Rush-Sedge Series (*Juncus* sp.)	All regions	4
Gulf Cordgrass Series (*Spartina spartinae*)	2a, 4a, 4b, 4c, 5, 6	3
Marshhay Cordgrass Series (*Spartina patens*)	4a, 4b, 4c	3
Saltgrass Series (*Distichlis spicata*)	5, 6, 7, 9, 10, 11	4
Smooth Cordgrass Series (*Spartina alterniflora*)	4a, 4b	3

that are recoverable to near-climax—A=less than 1000 hectates, B=1000-5000 hectares, C=5000-25,000 hectares, D=more than 25,000 hectares. Unpublished information from the Texas Natural Heritage Program, which represents a synthesis of data from federal, state, and major private conservation-oriented land owners, was the primary source used to determine ranks. Community types were ranked as endangered (1) if they received an A in two categories, threatened (2) if they received at least one A no D ranks, apparently secure (3) if they received no A and one or no D ranks, and secure (4) if they received two or more D ranks. These catagories were mutually exclusive for the community types listed in Tables 1-4.

Three community types are considered endangered (Table 5). These include one grassland within the Blackland and Fayette prairies, and two subtropical types of the Rio Grande delta. Most of the area formerly occupied by these community types has been converted to cropland (McMahan et al., 1984). Seven additional community types are considered threatened. All five of the tallgrass grasslands of the Blackland, Fayette, and Costal prairies are endangered or threatened, primarily due to conversion of these types to row crops.

TABLE 5.—Conservation ranking for endangered (1) and threatened (2) community types of Texas.

Community type	Total area[1]	Estimated number of relicts[2]	Number of relicts protected[3]	Relative threat of disturbance[4]	Conservation rank
American Beech-Southern Magnolia Series (*Fagus grandifolia-Magnolia grandiflora*)	C	C	B	A	2
Cottonwood-Tallgrass Series (*Populus deltoides*)	B	B	A	B	2
Gammagrass-Switchgrass Series (*Tripsacum dactyloides-Panicum virgatum*)	A	B	A	A	1
Little Bluestem-Brownseed Paspalum Series (*Schizachyrium scoparium-Paspalum plicatulum*)	B	B	B	A	2
Little Bluestem-Indiangrass Series (*Schizachyrium scoparium-Sorghastrum nutans*)	B	C	B	A	2
Longleaf Pine-Tallgrass Series (*Pinus palustris*)	C	C	B	A	2
Silveanus Dropseed Series (*Sporobolus silveanus*)	B	B	A	B	2
Texas Ebony-Anacua Series (*Pithecellobium flexicaule-Ehretia anacua*)	B	A	B	A	1
Texas Ebony-Snake-eyes Series (*Pithecellobium flexicaule-Phaulothamnus spinescens*)	B	B	B	A	2
Texas Palmetto Series (*Sabal texana*)	A	A	A	A	1

[1] A = less than 1000 hectares, B = 1000-5000 hectares, C = 5000-25,000 hectares, D = more than 25,000 hectares.
[2] A = 0-5, B = 6-20, C = 21-100, D = more than 100.
[3] A = 0-1, B = 2-5, C = 6-10, D = more than 100.
[4] A = extreme, B = moderate, C = probably none, D = none.

DISCUSSION

Several limitations of the plant community classification are apparent: (1) determination of the composition of late seral stage plant communities is difficult due to lack of relicts and lack of quantitative data; (2) many seral community types, which have come to dominate the contemporary landscape due to various cultural impacts, are not included in the classification; and (3) many plant associations are threatened or endangered, but are not included here because plant communities are only classified at the series level. Hence, the classification presented is dynamic and can be altered, pending improved knowledge of the vegetation of Texas. Development of an inclusive classification is an iterative process that will probably not be accomplished in the near future.

Conservation ranks are subject to change with increased knowledge and changing land use patterns. The ranking system is not meant to be dogmatically applied. Numerous indices have been proposed for setting priorities, and the conservation rank of a community is one of a number of criteria to consider (Tubbs and Blackwood, 1971; Trans, 1974; Gehlbach, 1975; Klopatek et al., 1981; Game and Peterken, 1984). Examples of community types that may become endangered or threatened because of changing land use patterns include East Texas bottomland forests, due to building of dams or building of levees and clearing for agriculture; East Texas upland forests and bogs, due to timber production activities; woodlands along the Balcones escarpment, due to urbanization caused by the growth of San Antonio, New Braunfels, San Marcos, Austin, Temple, and Waco; and barrier island grasslands due to expanding recreational and urban development.

Research Needs

Few comprehensive qualitative or quantitative surveys of natural resources within managed areas exist. Carls and Ludeke (1984) surveyed all state parks, but this analysis was based on qualitative secondary data provided by the Texas Parks and Wildlife Department. Smeins and Diamond (1986) surveyed all federal, state, and private-managed natural areas in central Texas, but this, again, was based on secondary data and the geographic scope of the study was limited. One of the purposes of the Texas Natural Heritage Program, now housed within the General Land Office, is to gather information on all managed natural areas in Texas. This data base is extremely useful as a synthesis of existing information, but it is not yet complete and partly based on secondary information, though qualitative surveys will be completed over time. The secondary qualitative data used in all of these cases is of undetermined reliability.

Published quantitative data on plant communities are incomplete. Regions that are especially lacking include the South Texas Plains, lower Rio Grande Valley, Edwards Plateau, and Rolling Plains. Data on riparian forests outside of the Piney Woods are generally lacking as are data on the ecophysiology and life history of important species. Also, the taxonomy of important species is in some cases controversial.

A long and continued history of overgrazing, cultivation, timber production, and other changes in land use makes reconstruction and recognition of late seral plant communities tentative, and the opportunity to study and conserve relatively natural vegetation is constantly diminishing. There is an immediate need for more quantitative studies on the composition, distribution, and ecology of the vegetation of Texas. These data then could be synthesized and incorporated into a revised classification and, together with more complete information about natural areas already protected, would serve to direct future conservation efforts.

Stewardship

Conservation of significant natural areas already under federal or state ownership or in private nature preserves is not guaranteed. Sometimes relict plant communities are not recognized, or are recognized but given a low priority in the overall management scheme. Even where nature preserves are established to maintain the integrity of relict plant communities, neglect due to lack of funds or improper management due to lack of expertise has in many cases caused degradation of the resource. Hence, there is a need to identify and manage significant natural areas on public lands, and to provide funds and expertise for management of private nature preserves. Private owners who are good land stewards have been, and continue to be, identified and honored by organizations such as The Nature Conservancy, but the fate of the native vegetation within private ownership is at best tentative.

Landscape Ecology

Considerable attention has been given to the problem of insularity of nature preserves and concomitant problems of long-term genetic isolation and the attenuation of recruitment and extinction relationships of species (Pickett and Thompson, 1978; Harris, 1984). The size of natural areas and their proximity to each other (degree of fragmentation) are important landscape considerations that influence these processes. Concepts borrowed from the theory of island biogeography indicate that, all else being equal, larger areas, or small areas with close neighbors, provide for increased diversity and dispersal potential and lower extinction rates (Diamond, 1975; Wilson and Willis 1975; Harris, 1984). An interesting approach toward solving the problem of habitat fragmentation and concomitant species extinction on small preserves would be management of corridors, such as highway right-of-ways and stream floodplains, for native vegetation in order to provide migration routes connecting natural areas (Ode, 1972). Thus, landscape considerations regarding the size and placement of nature preserves are important considerations. Unfortunately, we are far from achieving an integrated, biogeographic approach to natural area protection and management, and decisions usually must be made on a local, case-by-case basis (Godron and Forman, 1983).

Summary

The plant community classification presented in Tables 1-4 is the only state-wide classification at so fine a scale of resolution. Preliminary conservation ranks, based on rarity of relicts and current protection status, have been assigned to each community type. These should be subject to modification, pending acquisition of additional quantitative data, which are lacking for much of Texas. Significant natural communities on state and federal lands and private preserves are not always recognized or managed with conservation of the resource as the

primary goal. An analysis of the late seral stage communities already in public ownership or in private preserves would ensure that significant communities are recognized and would help in setting conservation priorities. Funds and expertise are needed for the proper management of existing preserves and the establishment of new preserves. A biogeographic approach toward natural area conservation would improve the probability for effective long-term protection, and conservationists should make landscape ecology an important consideration.

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INTRAPOPULATIONAL VARIATION IN TWO SAMPLES OF ARID-LAND FOXES

Jerry W. Dragoo, Jerry R. Choate, and Thomas P. O'Farrell
Museum of the High Plains, Fort Hays State University, Hays, Kansas 67601 (JWD, JRC); EG&G Energy Measurements, Inc., 130 Robin Hill Road, Goleta, California 93117 (TPO)

Abstract.—Intrapopulational variation was assessed for 14 cranial measurements in 205 specimens of the San Joaquin kit fox (*Vulpes macrotis mutica*) and 157 specimens of the swift fox (*Vulpes velox velox*). Variance components analysis revealed that less of the variability within both samples was the result of secondary sexual variation and age variation than of individual variation. Multivariate analysis of variance demonstrated significant differences among age categories but nonsignificant differences among sexes in both species. Tukey's studentized range tests showed that subadult males and females can be pooled with adult males and females for taxonomic study of geographic variation of these foxes. Old adults are significantly larger than subadults and adults, and should be analyzed separately. The two nominal species exhibit similar patterns of intrapopulational variation.

The taxonomic relationship between the swift fox (*Vulpes velox*) and the kit fox (*Vulpes macrotis*) is uncertain. Most authorities (Creel and Thornton, 1971; Egoscue, 1979; Packard and Bowers, 1970; Thornton and Creel, 1975) regarded them as separate species, but Hall (1981) classified them as subspecies of the same species (the name *V. velox* having priority) based on what was interpreted as gene flow between them in eastern New Mexico and western Texas (Rohwer and Kilgore, 1973).

Previous taxonomic studies on these foxes (cited above) dealt with relatively small samples from large geographic areas. The extent of variation within populations was poorly known, and this hindered attempts to evaluate the differences found in specimens from widely separated localities. To resolve this problem, large samples from restricted areas were needed.

Two such samples now are available. One was collected from a population of the endangered San Joaquin kit fox (*Vulpes macrotis mutica*) on the U.S. Department of Energy's (DOE) Naval Petroleum Reserve no. 1 (Elk Hills), Kern Co., California, and the other was obtained in western Kansas (*Vulpes velox velox*) with cooperation of the Kansas Fish and Game Commission.

Dragoo et al. (1986) characterized mensural variation of cranial measurements in the San Joaquin kit fox. The purpose of this study is to compare intrapopulational variation found in that taxon with that found in the sample of the swift fox from western Kansas. Data from these two large samples will be included in another manuscript detailing

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the systematic and evolutionary relationships of swift and kit foxes based on both morphometric and genetic analyses.

MATERIALS AND METHODS

We examined skulls of 362 arid-land foxes (205 of *V. m. mutica* and 157 of *V. v. velox*). Most (181) of the 205 kit fox skulls were from animals that had been live-trapped and ear-tagged between 1980 and 1986 and subsequently had been found dead of various causes. Twenty-four untagged animals were found dead incidental to other investigations. Researchers of the EG&G Energy Measurements survey team at Elk Hills characterized individuals as puppies, subadults, or adults when they were necropsied based on patterns of tooth eruption and wear, weight, and characteristics of the pelage. Live-trap, mark, and release data indicated that puppies were less than five months old, subadults were between five and 10 months old, and adults were more than 10 months old.

The utility of nine sutures as ageing criteria for the few specimens from California not aged at necropsy, and for all specimens from western Kansas, was tested based on the known-age specimens from California. The sutures tested were the occipito-parietal, squamoso-parietal, interparietal, interfrontal, coronal, basioccipito-basisphenoid, maxillary (palate), basisphenoid-presphenoid, and premaxillary-maxillary. These sutures have been used to age other carnivores (Orr et al., 1970); however, we found that all but two (basioccipito-basisphenoid and basisphenoid-presphenoid) are completely fused before the eruption of the permanent dentition in swift and kit foxes. Also, the interfrontal, coronal, and maxillary sutures sometimes separate when skulls are cleaned and dried. Therefore, only the basioccipito-basisphenoid and basisphenoid-presphenoid sutures were used to age specimens.

Waithman and Roest (1977) considered specimens adults if the basioccipito-basisphenoid suture was fused. We found that, in subadults, the basioccipito-basisphenoid suture is fused and the basisphenoid-presphenoid suture still is open. In adults, both sutures are fused. As adult foxes mature, the suture lines increasingly become indistinguishable. Therefore, we subdivided the adult age class into adults and old adults based on the distinguishability of these sutures.

Dental attrition and date of collection also were evaluated in borderline instances. Attrition of occlusal surfaces of the teeth is pronounced in certain old adults. Date of capture was considered because the San Joaquin kit fox and swift fox produce only one litter per year, the former in February (Morrell, 1972) and the latter in early April (Kilgore, 1969).

Specimens from Kansas were acquired from trappers and fur dealers during two harvest seasons (15 November through 15 January of 1981-82 and 1982-83). Therefore, no puppies were included in that sample and, for purposes of comparison, it was necessary to exclude the puppy age class from the California sample. Dragoo et al. (1986) previously ascertained that this age class was highly variable and not useful for taxonomic studies.

Fourteen cranial measurements (illustrated by Dragoo et al., 1986) were recorded to the nearest 0.1 mm using dial calipers: greatest length of skull (GLS)—from anterior tip of premaxillary to posterior point of inion (back of skull); nasal length (NL)—from anterior notch to tip of posterior extension of nasal; zygomatic breadth (ZB)—greatest distance across zygomata; breadth of braincase (BB)—maximal breadth of braincase across level of parietal-squamosal suture; postorbital constriction (PC)—least width across frontals at constriction behind postorbial processes; lyre breadth (LB)—distance between temporal ridges at frontal-parietal suture; palatal length (PL)—from anterior surface of premaxillary to posterior border of palate; alveolar length of maxillary toothrow (AL)—from anterior border of alveolus of P1 to posterior border of alveolus of M2; rostral breadth at first molar (RBM1)—breadth of rostrum across alveoli of M1; rostral breadth at canines

(RBC)—breadth of rostrum across alveoli of canines; greatest bullar width (GBW)—greatest width of bulla perpendicular to long axis of skull; greatest bullar length (GBL)—from sharp anterior end of tympanic bulla near pterygoid process diagonally to posterior end of bulla adjacent to paraoccipital process; bullar depth (BD)—from dorsal surface of external auditory meatus to bottom of bulla; external auditory meatus height (EAMH)—greatest height of external auditory meatus perpendicular to long axis of skull. All measurements were taken by one person (Dragoo) to minimize sampling error. These measurements have been used in morphometric studies of other canids (Nowak, 1979) and in previous investigations of swift and kit foxes (Waithman and Roest, 1977; Rowher and Kilgore, 1973).

We used the VARCOMP procedure of Statistical Analysis System (SAS) 84.2 (SAS Institute Inc., 1982) to determine the proportion of variation attributable to sex, age, sex by age interaction, and "residual" (variation resulting from factors other than sex or age). Descriptive statistics ($\bar{X}$, range, SE, and CV) were determined for each variable in each age class for both sexes using the UNIVARIATE procedure of SAS. Animals of unknown sex were not included because one purpose of this analysis was to determine whether sexes could be pooled for taxonomic study of swift and kit foxes. When a particular measurement could not be taken, that specimen was excluded from the sample for that measurement but was included for other measurements.

For reasons enunciated by Willig et al. (1986), we used multivariate analysis of variance (procedure GLM—SAS Institute Inc., 1982) to determine whether overall group differences between sexes, among age categories, or among a combination of sexes and age categories (sex by age interaction) were significant. Tukey's studentized range test (HSD) of the TUKEY option of the GLM procedure then was used to group nonsignificant subsets of sexes within each age class and age classes within each sex while protecting the experimentwise error rate for multiple comparisons. Only 264 specimens were used for this analysis because specimens with missing measurements were not included.

RESULTS

The two ways of partitioning variance (variance components and sums of squares) of the VARCOMP procedure yielded comparable results. Therefore, only variance components data are listed (Table 1). Variance components estimates generally were larger than sums of squares except for "residual," which was reversed. "Residual" (which we interpreted as individual variation and sampling error) accounted for well over one-half of the mensural variation in both samples. Less than 16 percent of the mensural variation in the samples was the result of sexual dimorphism. Means for mensural variation resulting from age were higher when partitioned by variance components (18 percent in *V. velox* and 27 percent in *V. macrotis*) than when partitioned by sums of squares (6 percent and 19 percent, respectively).

Descriptive statistics for each sex and age class in the samples are given in Table 2. When these samples are compared side by side, *V. macrotis* appears to have a slightly longer skull and broader braincase than *V. velox*. *V. macrotis* also has deeper bullae and a larger external auditory meatus. The bullae are approximately the same length and width in the two nominal species. *V. velox* has slightly longer nasals and a wider rostrum at the canines and molars. In old adults of both taxa, lyre

TABLE 1.—Percent contribution to the total variance of two populations of arid-land foxes (*Vulpes velox* and *V. macrotis*) by sex (S), age (A), sex by age interaction (S × A), and residual (R) for 14 morphometric characters.

	Variance Components							
	S		A		S × A		R	
	velox	*macrotis*	*velox*	*macrotis*	*velox*	*macrotis*	*velox*	*macrotis*
GLS	17.52	30.61	61.29	45.59	0.00	3.46	21.19	20.34
NL	24.92	10.88	32.24	23.23	0.00	12.02	42.84	53.87
ZB	34.51	19.75	5.49	40.83	0.00	7.63	60.00	31.79
BB	18.59	13.50	4.94	19.92	0.00	1.06	76.47	65.52
PC	7.07	1.75	10.37	22.20	0.00	2.43	82.56	73.62
LB	11.18	10.35	27.33	52.84	0.00	6.27	61.49	30.54
PL	24.69	21.57	39.92	46.97	0.00	1.08	35.39	30.38
AL	28.19	23.10	28.72	35.60	0.00	4.93	43.09	36.37
RBM1	22.05	23.99	17.00	25.84	0.00	4.41	60.95	45.76
RBC	22.48	27.61	22.83	20.86	0.00	4.29	54.69	47.24
GBW	0.00	1.72	2.64	12.72	0.00	0.00	97.36	85.56
GBL	1.10	0.94	1.75	20.09	0.00	13.04	97.15	65.93
BD	0.00	5.76	0.00	11.75	6.88	0.00	93.12	82.49
EAMH	10.00	3.33	2.22	3.33	0.00	0.00	87.78	93.34
MEAN	15.88	13.92	18.34	27.27	0.49	4.33	65.29	54.48

breadth usually was less than 10 mm, greatest length of skull generally was greater than 120 mm, and postorbital constriction became narrower, proportionally, as length of skull increased. These characters also may be used to age specimens.

Multivariate analysis of variance revealed that differences among age categories were significant ($P > F = 0.0001$ in *V. macrotis,* $P > F = 0.01$ in *V. velox*, both based on Wilks' criterion for calculation of exact F) but that differences between sexes or resulting from sex by age interaction were nonsignificant ($P > 0.05$). Tukey's studentized range tests (Table 3) grouped adult males and females in the same nonsignificant subset for all but one multiple comparison (GLS in *V. macrotis*), and grouped subadult males and females in the same nonsignificant subset for all multiple comparisons. The four sex and age classes (subadult and adult males and females) were grouped in the same nonsignificant subset for 12 multiple comparisons for *V. velox* and for four multiple comparisons for *V. macrotis*. The F values for three measurements (GBW, GBL, and BD) for *V. velox* were less than 1.0 and were regarded as nonsignificant.

DISCUSSION

Grinnell et al. (1937) presented a table of measurements comparing males with females and demonstrated, using descriptive statistics, that

TABLE 2.—Discriptive statistics for each sex and age class of two samples of arid-land foxes. Numbers under the age column represent age classess: 2, subadults; 3, adults; and 4, old adults.

		N		Mean		2 SE		Range		CV	
Age	Sex	*velox*	*macrotis*	*velox*	*macrotis*	*velox*	*macrotis*	*velox*	*macrotis*	*velox*	*macrotis*
						Greatest length of skull					
2	female	9	22	107.5	109.8	0.49	0.97	106.4-108.8	102.9-113.0	0.68	2.07
2	male	3	9	108.6	110.4	0.07	1.19	108.5-108.6	107.5-113.6	0.05	1.62
3	female	68	82	112.2	113.2	0.48	0.64	109.0-117.0	101.2-118.4	1.77	2.55
3	male	62	44	114.5	116.2	0.59	0.81	109.2-118.6	109.7-119.9	2.02	2.31
4	male	1	23	120.0	122.5		0.83	120.0	120.1-126.8		1.62
						Nasal length					
2	female	10	22	32.9	34.2	0.90	0.52	30.0- 34.4	31.6- 36.5	4.30	3.55
2	male	2	10	34.4	33.5	1.20	1.01	33.2- 35.6	31.6- 36.9	4.93	4.79
3	female	70	83	35.2	35.1	0.47	0.43	25.7- 39.4	28.5- 38.8	5.60	5.61
3	male	61	44	36.7	36.2	0.44	0.52	32.7- 41.4	32.7- 40.1	4.69	4.78
4	male	1	23	38.1	38.1		0.60	38.1	35.9- 40.8		3.76
						Zygomatic breadth					
2	female	8	18	61.8	57.1	1.06	0.83	59.0- 63.3	54.4- 61.4	2.43	3.08
2	male	2	8	62.8	56.8	1.20	1.53	61.6- 64.0	54.4- 60.5	2.70	3.80
3	female	59	76	62.4	59.8	0.51	0.50	51.2- 65.8	48.2- 63.8	3.17	3.63
3	male	49	43	64.2	61.8	0.52	0.65	60.2- 67.6	54.8- 65.1	2.81	3.45
4	male	1	19	65.5	64.4		0.59	65.5	61.7- 66.8		1.99
						Breadth of braincase					
2	female	9	19	42.0	42.9	0.67	0.46	40.0- 43.3	41.4- 44.6	2.41	2.34
2	male	3	9	42.1	42.8	0.17	0.43	41.9- 42.3	41.9- 43.8	0.49	1.52
3	female	67	80	42.3	43.2	0.22	0.20	40.3- 45.5	41.2- 45.3	2.13	2.11
3	male	59	44	42.9	43.6	0.23	0.23	41.2- 45.0	41.7- 45.1	2.03	1.77
4	male	1	22	42.3	44.5		0.45	42.3	42.7- 46.3		2.40

TABLE 2.—*Continued*

Postorbital constriction											
2	female	10	22	23.7	22.5	0.60	0.50	22.1-24.8	20.6-25.0	4.01	5.23
2	male	3	10	23.6	22.7	0.87	0.57	22.7-24.1	21.1-24.0	3.21	3.95
3	female	72	83	23.1	21.6	0.32	0.21	19.6-26.1	19.8-23.8	5.88	4.47
3	male	61	44	23.1	21.2	0.31	0.33	20.0-25.7	19.3-23.4	5.23	5.10
4	male	1	23	21.9	21.1		0.49	21.9	19.0-23.3		5.52
Lyre breadth											
2	female	9	22	16.0	14.4	1.82	1.17	11.3-19.2	10.5-20.1	17.11	19.17
2	male	3	10	14.3	15.2	1.97	1.43	12.4-15.7	11.4-20.0	11.93	14.81
3	female	69	82	14.0	9.7	0.57	0.70	9.3-19.8	4.2-22.4	16.90	32.53
3	male	61	43	13.2	7.7	0.57	0.87	9.2-18.4	3.6-16.9	16.83	37.16
4	male	1	23	7.9	4.0		0.75	7.9	1.2-7.2		44.23
Palatal length											
2	female	10	22	53.8	54.5	0.52	0.69	52.8-55.3	51.0-56.9	1.53	2.97
2	male	3	10	55.3	54.7	0.44	0.87	54.9-55.6	52.6-57.1	0.68	2.50
3	female	73	83	56.0	56.1	0.32	0.38	53.5-59.0	49.0-59.8	2.48	3.09
3	male	64	43	57.5	57.2	0.42	0.48	52.4-60.8	53.4-60.5	2.93	2.73
4	male	1	23	59.4	60.6		0.58	59.4	58.7-64.6		2.31
Alveolar length of maxillary toothrow											
2	female	10	22	41.6	41.1	0.53	0.51	40.5-42.6	38.6-43.2	2.01	2.94
2	male	3	10	42.8	41.1	0.35	0.86	42.1-43.2	39.1-43.0	1.42	3.30
3	female	73	83	42.9	42.2	0.26	0.29	40.2-45.8	38.8-45.4	2.54	3.12
3	male	65	43	44.0	43.3	0.29	0.38	40.4-47.1	39.3-45.1	2.68	2.88
4	male	1	22	44.2	45.2		0.41	44.2	43.1-46.8		2.14
Rostral breadth at first molar											
2	female	10	22	33.5	30.6	0.47	0.33	32.1-35.0	29.6-33.3	2.21	2.55
2	male	3	10	34.6	30.6	0.35	0.73	34.3-34.9	29.1-32.5	0.87	3.76
3	female	72	83	34.4	31.1	0.24	0.20	32.6-37.6	28.2-33.0	2.93	2.95
3	male	63	44	35.0	31.9	0.23	0.35	32.8-36.8	29.7-34.5	2.60	3.63
4	male	1	23	35.8	33.1		0.39	35.8	31.8-35.5		2.84

TABLE 2.—*Continued*

					Rostral breadth at canines						
2	female	10	22	17.3	17.3	0.20	0.32	16.6- 17.6	16.1- 19.9	1.87	4.40
2	male	3	10	18.1	17.4	0.30	0.42	17.8- 18.3	16.1- 18.1	1.46	3.78
3	female	73	83	17.9	17.5	0.13	0.14	16.4- 19.0	15.6- 19.2	3.14	3.62
3	male	63	44	18.3	18.1	0.15	0.23	16.8- 19.8	16.3- 19.9	3.18	4.20
4	male	1	23	19.3	19.0		0.25	19.3	17.8- 20.1		3.19
					Greatest bullar width						
2	female	10	21	14.2	14.5	0.28	0.35	13.6- 14.9	12.6- 15.8	3.16	5.56
2	male	3	10	14.5	14.4	0.84	0.36	13.7- 15.0	13.7- 15.4	4.98	3.91
3	female	69	83	14.6	14.6	0.16	0.15	13.2- 16.3	12.9- 16.6	4.66	4.56
3	male	60	44	14.5	14.6	0.16	0.14	13.3- 15.7	13.6- 15.6	4.17	3.29
4	male	1	23	14.7	15.0		0.25	14.7	14.1- 16.2		3.94
					Greatest bullar length						
2	female	10	21	21.2	21.1	0.31	0.33	20.6- 21.9	19.7- 22.4	2.34	3.61
2	male	3	10	21.6	20.6	0.70	0.34	21.2- 22.3	20.0- 21.8	2.82	2.59
3	female	69	82	21.6	21.2	0.16	0.17	19.5- 23.2	20.1- 23.3	3.01	3.57
3	male	60	44	21.6	21.5	0.18	0.23	20.2- 23.1	20.0- 23.4	3.28	3.55
4	male	1	23	21.5	22.3		0.31	21.5	21.2- 23.6		3.36
					Bullar depth						
2	female	10	21	11.1	11.9	0.38	0.25	10.0- 12.1	10.8- 12.7	5.50	4.87
2	male	3	10	11.6	12.1	0.23	0.53	11.4- 11.8	11.1- 13.9	1.72	7.01
3	female	69	83	11.3	12.1	0.14	0.13	10.1- 12.8	10.4- 13.6	4.95	4.88
3	male	60	44	11.4	12.2	0.14	0.15	10.1- 12.7	11.3- 13.6	4.60	4.16
4	male	1	23	11.5	12.6		0.25	11.5	11.5- 13.9		4.75
					External auditory meatus height						
2	female	10	21	7.3	7.8	0.20	0.11	6.9- 8.0	7.3- 8.2	4.46	3.35
2	male	3	10	7.2	7.7	0.29	0.15	7.0- 7.5	7.4- 8.1	3.48	3.10
3	female	69	83	7.3	7.8	0.07	0.07	6.7- 8.1	7.3- 8.6	3.84	3.85
3	male	61	44	7.5	7.9	0.07	0.09	6.7- 8.2	7.3- 8.6	3.69	3.72
4	male	1	23	7.4	7.9		0.12	7.4	7.4- 8.5		3.49

TABLE 3.—Variation among sex and age classes for 14 cranial measurements of two populations of arid-land foxes. Numbers represent age classes: 2, subadults; 3, adults; 4, old adults. Horizontal lines identify nonsignificant subsets as determined by Tukey's studentized range test. The *F* value for each variable is given in parentheses.

Greatest length of skull			Nasal length	
V. velox	(*F*=24.97)	4♂ 3♂ 3♀ 2♂ 2♀	(*F*=6.16)	4♂ 3♂ 3♀ 2♂ 2♀
V. macrotis	(*F*=63.85)	4♂ 3♂ 3♀ 2♂ 2♀	(*F*=14.69)	4♂ 3♂ 3♀ 2♀ 2♂
Zygomatic breadth			Breadth of braincase	
V. velox	(*F*=6.50)	4♂ 3♂ 2♂ 3♀ 2♀	(*F*=3.48)	3♂ 4♂ 3♀ 2♂ 2♀
V. macrotis	(*F*=40.07)	4♂ 3♂ 3♀ 2♀ 2♂	(*F*=9.51)	4♂ 3♂ 3♀ 2♂ 2♀
Postorbital constriction			Lyre breadth	
V. velox	(*F*=1.01)	2♀ 2♂ 3♀ 3♂ 4♂	(*F*=3.51)	2♀ 3♀ 2♂ 3♂ 4♂
V. macrotis	(*F*=6.83)	2♂ 2♀ 3♀ 3♂ 4♂	(*F*=42.76)	2♂ 2♀ 3♀ 3♂ 4♂
Palatal length			Alveolar length of maxillary toothrow	
V. velox	(*F*=11.44)	4♂ 3♂ 3♀ 2♂ 2♀	(*F*=9.11)	4♂ 3♂ 3♀ 2♂ 2♀
V. macrotis	(*F*=40.18)	4♂ 3♂ 3♀ 2♂ 2♀	(*F*=31.36)	4♂ 3♂ 3♀ 2♂ 2♀
Rostral breadth at first molar			Rostral breadth at canines	
V. velox	(*F*=4.17)	4♂ 3♂ 2♂ 3♀ 2♀	(*F*=7.64)	4♂ 3♂ 2♂ 3♀ 2♀
V. macrotis	(*F*=20.04)	4♂ 3♂ 3♀ 2♀ 2♂	(*F*=20.94)	4♂ 3♂ 3♀ 2♂ 2♀
Greatest bullar width			Greatest bullar length	
V. velox	(*F*=0.80)	4♂ 3♀ 3♂ 2♂ 2♀	(*F*=0.55)	2♂ 3♂ 3♀ 4♂ 2♀
V. macrotis	(*F*=2.67)	4♂ 3♀ 3♂ 2♀ 2♂	(*F*=10.39)	4♂ 3♂ 3♀ 2♀ 2♂
Bullar depth			External auditory meatus height	
V. velox	(*F*=0.21)	2♂ 4♂ 3♂ 3♀ 2♀	(*F*=1.85)	3♂ 4♂ 2♀ 3♀ 2♂
V. macrotis	(*F*=4.88)	4♂ 3♂ 3♀ 2♂ 2♀	(*F*=2.40)	4♂ 3♂ 3♀ 2♀ 2♂

males were slightly larger than females. Our results (Table 2) show the same trend, especially in the adult age class. However, the differences in size between these age classes were not significant in our large samples of either the swift fox or the kit fox. Therefore, males and females can be pooled for taxonomic comparison of these samples with other samples of arid-land foxes, as previously suggested by Rohwer and Kilgore (1973), Waithman and Roest (1977), and Stromberg and Boyce (1986).

Lyre breadth has been used by previous investigators both as a taxonomic character (Waithman and Roest, 1977) and as an age character (Grinnell et al., 1937; Waithman and Roest, 1977). The results of this study demonstrate that lyre breadth is highly variable and is of little use as a taxonomic character. Morever, although lyre breadth decreases concomitant with development of a sagittal crest as foxes get older, this is not an accurate criterion by which to age foxes.

Because we omitted the puppy age class (which eliminated the lower range of measurements) from the kit fox sample, the results of the Tukey's studentized range test indicated fewer significant differences between adult males and old adult males and more significant differences between adult males and the other sex and age classes than reported by Dragoo et al. (1986). Measurements of the one old adult male in the Kansas sample overlapped with many measurements of adult males; however, when a larger sample of old adults is available, it should be analyzed separately from adults and subadults (Dragoo et al., 1986). Results of analysis of our sample of swift foxes support the assertion by Dragoo et al. (1986) that measurements of subadult males and females can be pooled with those of adult males and females for analysis of taxonomic relationships so long as caution is taken to avoid excessive sample bias.

Say (1823) described the swift fox and, 75 years later from a locality 2240 kilometers away, Merriam (1888) described the kit fox. The results of this study corroborate Merriam's (1888) assertion that kit foxes have narrower rostra and larger (deeper) bullae than swift foxes. In most other respects, the two species exhibit similar patterns of intrapopulational variation. Understanding of these patterns will be useful in evaluating variation among populations of the two nominal species and between the two species.

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Present address of Dragoo: Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843.

COMPARISON OF CANOPY POSITION AND OTHER FACTORS ON SEEDLING GROWTH IN *ACACIA SMALLII*

R. J. Lohstroh and O. W. Van Auken
Division of Life Sciences, The University of Texas at San Antonio,
San Antonio, Texas 78285

Abstract.—A factorial field experiment was designed to measure the affect of canopy position, root competition, added nutrients, and herbivory on the growth of *Acacia smallii* Isley (huisache). Maximum growth occurred in the open (full sunlight) compared to beneath the mature *A. smallii* canopy (shade), but the other factors tested had no significant effect. Mean dry weight of *A. smallii* grown in seven of eight canopy treatments decreased during the experiment, whereas *A. smallii* in all open-area treatments (full sunlight) increased in mean dry weight. This study confirms previous greenhouse experiments that showed the importance of high levels of irradiance to this colonizer. *Key words:* huisache; light intensity; shade; trenching; competition; added nutrients; herbivory.

Four factors that are important for the establishment of plant seedlings are light intensity, root competition, available nutrients, and herbivory (Harper, 1977). How all of these factors affect the growth of *Acacia smallii* Isley (huisache), an early successional species, are mostly unknown (Van Auken and Bush, 1985). A wide variety of plants have been tested for light requirements and shown to be sun or shade plants (Boardman, 1977; Bazzaz, 1979). In a greenhouse experiment, Bush and Van Auken (1986a) showed that *A. smallii* was shade intolerant. In addition, Van Auken et al. (1985) showed that *A. smallii* did not respond to added nitrogen but did grow better when supplemented with other nutrients.

Herbivory is another factor that can affect community dominance (Harper, 1977). In California, herbivores were responsible for destroying approximately seven percent of the total leaf area of *Eriodictyon californicum* (Johnson et al., 1984). Gilbert (1985) observed that stands of *Celtis pallida* (desert hackberry) were partially or completely defoliated by *Libytheana bachmanii* (snout butterfly) and, consequently, were replaced by *Celtis laevigata* (Texas sugarberry).

Plants also compete for water and nutrients (Harper, 1977). Competition is least during early community development where plant density is low; however, as a community matures, density and competition between root systems increase (Weaver and Clements, 1966; Smith, 1980). The ability of a species to compete for resources below ground certainly influences its ability to survive and its position in a community.

This field study was designed to examine the affect of canopy position, nutrient addition, herbivory, and root competition on the growth of *A. smallii* seedlings.

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METHODS

Acacia smallii seeds were collected in May, 1984, from trees located along the San Antonio River, Bexar County, Texas. The seeds were scarified for 15 minutes in concentrated sulfuric acid and then rinsed thoroughly with distilled water. Seeds were sown in pots containing 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, 1986b). Rainfall data were taken from the NOAA local climatological data summary (NOAA, 1984).

Seven weeks after sowing, plants were sized according to height and vigor and transplanted one per pot. Three weeks later, 119 plants were again sized; seven plants were kept in the greenhouse and the remaining plants were transplanted to a field site along the San Antonio River. Seven plants, randomly selected, were placed into each of the 16 treatments. Plants in the field, as well as the plants in the greenhouse, were given 300 milliliters of distilled water approximately twice per week before zero-time measurements were taken. Four weeks were allowed for equilibration before zero-time measurements were taken. The greenhouse plants were harvested for zero-time measurements by cutting at the cotyledon scars and drying the plants in an oven (65-70° C) to a constant weight.

The experimental design was 2^4 factorial with canopy position (under the canopy or in the open), nutrients (added or not added), root competition (roots present or trenching, that is, no woody plant roots), and herbivory (herbivores present or insecticide treatment, that is, no herbivores) as factors. With all combinations, there were 16 total treatments. The canopy position was beneath five mature *A. smallii* trees and the open area was adjacent. Mean light intensities were 515 $\mu\mathrm{Mm}^{-2}\cdot\mathrm{sec}^{-1}$ under the canopy and 2173 $\mu\mathrm{Mm}^{-2}\cdot\mathrm{sec}^{-1}$ 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) added two weeks after planting and then approximately every three 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 zero-time measurements were taken. Plants were cut at the cotyledon scars and dry weights were measured. Data were statistically analyzed by an analysis of variance procedure and means were separated using the Least Significant Difference test (Steel and Torrie, 1980; SAS Institute, 1982).

RESULTS

Of the main factors tested including canopy position, herbivory, competition, and added nutrients, only canopy position showed significant differences (ANOVA, $F = 15.51$, $P < 0.0001$, Fig. 1). All two-way and three-way interactions were tested with ANOVA and there were no significant differences ($F = 0.00$-1.75, $P > 0.05$). Mean dry weight for *Acacia smallii* plants grown in the open (full light) was 1.79 ± 0.99

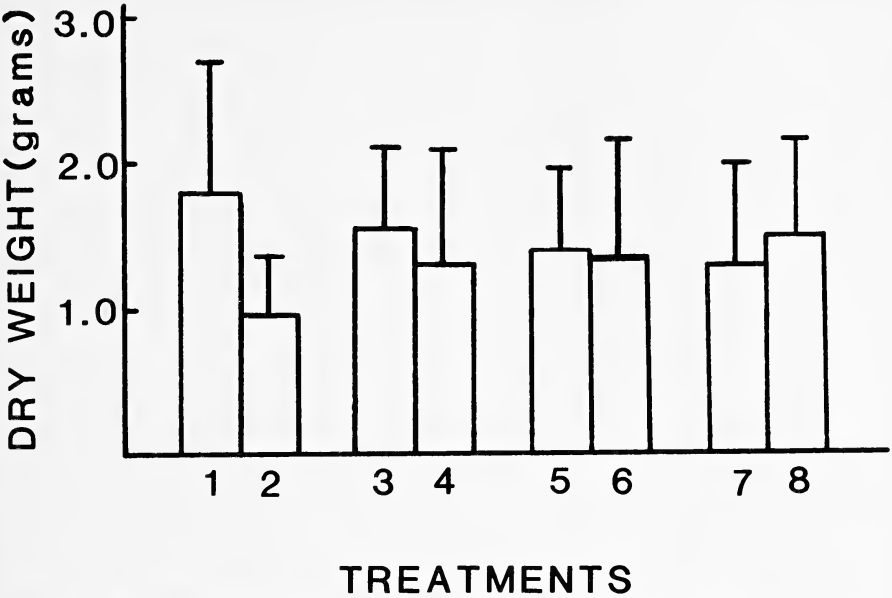

FIGURE 1. Bar graph showing mean dry weight (± 1 SD) of *Acacia smallii* grown for 12 weeks under various field conditions. Treatments were as follows: 1, open; 2, under canopy; 3, herbivory; 4, no herbivory; 5, competition; 6, no competition (trenched plots); 7, nutrient supplement; 8, no nutrients added. Plants in treatment 1 were significantly different from those in treatment 2 (ANOVA, LSD, $P < 0.05$). There were no significant differences between the other treatments.

grams, whereas the mean dry weight of those under the canopy (shade plants) was 0.96 ± 0.44 grams. Mean dry weight of the zero-time plants was 1.07 ± 0.26 grams. Canopy plants were slightly lower in mean dry weight than the zero-time plants ($P > 0.05$).

Means of all treatments were separated using the least significant difference test (Table 1). The main differences are in canopy position. Other differences should not be considered because the major effects were not significant when tested with ANOVA.

Rainfall during the experiment was 62 percent greater than normal and did not seem to be a factor. There were only three weeks (5, 10, and 11) during the experiment that did not have any rainfall and plant mortality was only two percent during the experiment (Fig. 2). In addition, the mortalities occurred in the canopy treatments and they did not occur during brief periods of drought.

DISCUSSION

During most successional events, biotic and abiotic conditions change (Stevens and Walker, 1970; Brady, 1974; Armson, 1977; Gorham et al., 1979). Surface light-intensity is high early in succession and decreases as

TABLE 1. Mean aboveground dry weight (± 1 SD) for *Acacia smallii* grown in 16 treatments and zero-time measurements. Mean values followed by the same letter are not significantly different (ANOVA and Least Significant Difference Test $P > 0.05$).

Treatment	Dry-weight (grams)
Zero time	1.07 ± 0.27AB
Under canopy, herbivory, competition, nutrients	0.81 ± 0.43A
Under canopy, herbivory, competition, no nutrients	0.97 ± 0.30AB
Under canopy, herbivory, no competition, nutrients	0.75 ± 0.36A
Under canopy, herbivory, no competition, no nutrients	1.05 ± 0.60AB
Under canopy, no herbivory, competition, nutrients	1.15 ± 0.61AB
Under canopy, no herbivory, competition, no nutrients	0.99 ± 0.32AB
Under canopy, no herbivory, no competition, nutrients	1.04 ± 0.46AB
Under canopy, no herbivory, no competition no nutrients	0.98 ± 0.44AB
Open, herbivory, competition, nutrients	1.16 ± 0.27AB
Open, herbivory, competition, no nutrients	1.72 ± 0.74BCD
Open, herbivory, no competition, nutrients	1.74 ± 1.22BCD
Open, herbivory, no competition, no nutrients	1.75 ± 0.61BCD
Open, no herbivory, competition, nutrients	2.15 ± 0.94CD
Open, no herbivory, competition, no nutrients	2.04 ± 0.85CD
Open, no herbivory, no competition, nutrients	1.32 ± 1.37ABC
Open, no herbivory, no competition, no nutrients	2.47 ± 1.46D

forest community development proceeds (Bazzaz, 1979). Usually soil nitrogen is low during the early stages of succession and increases in time (Gorham et al., 1979). Consequently, colonizers are usually sun plants (heliophytes) tolerant of low soil nitrogen, whereas species of mature communities are usually shade plants (sciophytes) that require higher levels of soil nitrogen (Bormann, 1953; Grime, 1965; Loach, 1967; Ormsbee et al., 1976).

Van Auken and Bush (1985) showed that *Acacia smallii* occured early during secondary succession on river terraces in southern Texas. In addition, they showed that *A. smallii* was a sun plant (Bush and Van Auken, 1986a). *Acacia smallii* is also tolerant of low soil nitrogen (Van Auken et al., 1985), and soil nitrogen increased during this successional sequence (Bush and Van Auken, 1986b). However, the above studies were either field observations or greenhouse experiments. The present experimental field study showed that canopy position was the most important of the factors evaluated concerning establishment and growth of *Acacia smallii.* Seedlings planted in the open grew 1.86 times faster than those under the *A. smallii* canopy. This confirms the previous light-limited growth experiments carried out in the greenhouse and the proposed successional position of *A. smallii.*

Other factors examined, including competition, nutrient supplements, and herbivory, did not cause significant changes in *A. smallii* growth. Competition for soil-borne resources, mainly water and nutrients, can

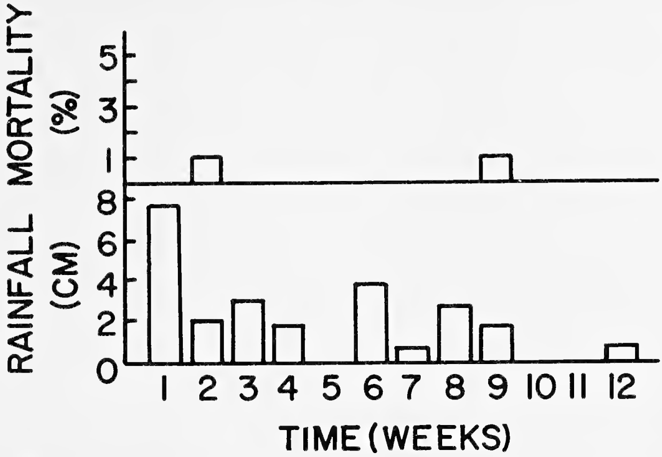

FIGURE 2. Rainfall and mortality bar graph of *Acacia smallii* seedlings planted in the field.

play a significant role in establishment and subsequent growth of species (Harper, 1977). Trenching can quite effectively eliminate root competition from study plots (Ehrenfeld, 1980; Horn, 1985). We did not see a difference in *A. smallii* 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 one or the other species (Harper, 1977). Cohn and Van Auken (unpublished results) showed significant growth reduction of *A. smallii* by *Cynodon dactylon* (bermuda grass) in a greenhouse study. Similar studies with *Prosopis glandulosa* (honey mesquite) and various grasses had the same results (Glendening and Paulsen, 1955; Van Auken and Bush, 1987).

Nutrient additions were not expected to have a great effect on the growth of *A. smallii* because of previous studies (Van Auken et al., 1985). However, because of the higher levels of nitrogen and carbon found below the *A. smallii* canopy, a nutrient treatment was included. Additional nitrogen in the canopy soil could have ameliorated the growth of *A. smallii* in spite of the shading effects caused by the canopy. The 20 percent decrease in growth of *A. smallii* in the open when nutrients were added was probably the result of 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 *A. smallii* 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 fall growing season might show significant growth reduction due to herbivory.

Although many factors may effect seedling establishment and growth of woody plants, the present field study identified seedling position relative to the canopy as the most important. Canopy shade inhibits *A. smallii* growth whereas the full sun of open areas promotes it. Canopy shade may be the major environmental variable required to explain the lack of *A. smallii* seedlings under the *A. smallii* canopy. *Acacia smallii* appears to be a heliophyte and early colonizer of old-fields and overgrazed grasslands of southern Texas and associated areas.

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NATURAL HISTORY SKETCHES, DENSITIES, AND BIOMASS OF BREEDING BIRDS IN EVERGREEN FORESTS OF THE RIO GRANDE, TEXAS, AND RIO CORONA, TAMAULIPAS, MEXICO

FREDERICK R. GEHLBACH
Department of Biology, Baylor University, Waco, Texas 76798

ABSTRACT. Comparative aspects of life history, including weights and densities, are presented for 24 breeding species at the Rio Grande in Texas and 40 at the Río Corona, in Tamaulipas, 18 of which are the same. The information suggests greater stability with a greater density of birds, especially passerines, and greater ecological influence of all breeding species at the Río Corona. Avian biomass is 2.7 times larger at the Río Corona, where wet-season rainfall is 2.5 times greater and may account for the inter-site difference through increased primary productivity. *Key words*: avifaunas; life histories; densities; biomass.

Over two decades I studied breeding birds at the Santa Ana National Wildlife Refuge on the Rio Grande, Texas, and near Guemez, Tamaulipas, on the Río Corona (Gehlbach et al., 1976; Gehlbach, 1981). Mature evergreen forest at the two locales, 330 kilometers apart, was essentially the same; for example, the tree stratum averaged 16.1 and 17.8 meters (m) tall, 29.0 and 33.1 centimeters (cm) in diameter, and contained 161 and 140 trees per hectare with species diversities ($H'\log_2$) of 2.43 and 2.31, respectively. However, avifaunas were temperate (Rio Grande) and tropical (Río Corona) in nature. Unfortunately, study plots at the Río Corona were destroyed by bulldozing in 1979-1980, so my general investigation of climate and vegetation in relation to avifaunal dynamics ceased in 1978. I here present life history sketches of breeding birds as background to brief, inter-site comparisons of avifaunal biomass and density.

METHODS

Investigations at each locale centered on two, lineal, eight-hectare plots in riparian evergreen forest, bordered by thorn woodland and mesquite grassland on the nonriver side. Breeding (April, June) and winter (December-January, March) community structures were examined, and the habits of breeding birds observed. The latter are categorized as making local movements (LM, absent for a few days or weeks but not the entire season), being migratory (M, absent in the non-breeding season), or resident (R, present in slightly varying numbers year-round). Nomenclature follows the 1983 edition of the "Check-list of North American Birds" except for *Vireo flavoviridis* (*sensu* Johnson and Zink, 1985).

Mean weights are based on personal captures and personally examined museum specimens from the region unless credited otherwise. The mean population densities plus or minus one standard deviation concern adults per eight hectares, calculated from four seasonal or eight total spot-map censuses per plot, three to five consecutive days each, in the period 1973-1978. Biomass is mean weight times mean density per species, summed for all species per season per site, except that ducks and kingfishers are excluded because they were not seen to feed in the forest.

BREEDING SPECIES

Black-bellied whistling-duck (*Dendrocygna autumnalis*), 838 grams (E. Bolen, personal communication). —CORONA: LM; 2.1 ± 1.3 in April, June; four fledglings on three days in June 1976; nesting likely just outside plots. GRANDE: LM; June 1974 nest with eggs 3.5 m high in broken limb of tepeguaje (*Leucaena pulverulenta*); otherwise absent. Some winter near both study locales.

Muscovy duck (*Cairina moschata*), ca. 2000 grams (literature).—CORONA:LM; absent December-January; 8-10 sporadically in March; 2.3 ± 1.6 in April, June. Nest not located, but birds persistent in forest interior, April and June.

Gray hawk (*Buteo nitidus*), 528 grams N = 13.—CORONA: R (1.7 ± 0.7). Defended nest, contents uncertain, in June 1973; another with two feathered nestlings, June 1976; single dependent fledgling, June 1976. Nests 15 m high in coma (*Bumelia lanuginosa*) crown, 175 m from river, and 18 m high in upper half of Montezuma cypress (*Taxodium mucronatum*) at river bank; both nests about 35 cm diameter, similar in aspect to those of *B. platypterus* in central Texas (Bush and Gehlbach, 1978). GRANDE: visitor; immature April 1977, June 1975; adult June 1977, which suggests nesting in the region.

Plain chachalaca (*Ortalis vetula*), 563 grams (W. Marion, personal communication).—CORONA: R(8.0 ± 4.2). Notably warier than at Rio Grande; mostly in tree crowns, rarely on ground; nests undiscovered. At 0800 in April, six flocked with eight great kiskadees, green jays, and altamira orioles and ate fruit 15 m high in coma and brasil (*Condalia hookeri*). GRANDE: R; 10-16 before 1977 when fed grain, 5-9 thereafter (10.5 ± 3.3). Commonly on ground, less so in shrubs and trees where certain leaves as well as fruits are eaten. Nests, two m (eggs) and 10 m (contents uncertain) high in granjeno (*Celtis pallida*) and brasil, respectively, June 1974, 1976; fledglings 18 June 1976 (see Marion and Fleetwood, 1978).

Red-billed pidgeon (*Columba flavirostris*), 244 grams, N = 18.—CORONA: LM; December-March birds flock and sun in tree crowns (11.1 ± 3.6); nesting population is but 5.3 ± 0.9 in April, June. Persistent singing from ebony (*Pithecellobium flexicaule*) crowns in April and June, copulation 8 April 1974; nests not located. GRANDE: LM; absent December-January; five appeared 25 March 1978 but disappeared the next day. Nest 12 m high in ebony crown, contents uncertain, June 1974; calling adult June 1976, but no mate or nest located (0.5 ± 0.7).

White-winged dove (*Zenaida asiatica*), 159 grams N = 16.—CORONA: M (6.0 ± 2.3). Earliest return 11 April 1974. Three nests with two feathered nestlings each in huisache (*Acacia farnesiana*), 3-5 m high, June 1973 on forest-woodland border. These trees were bulldozed in 1975; doves visited plots but did not nest thereafter. GRANDE: M; earliest return 4 April 1977, but a few sometimes winter in region. Nests in small trees of the forest-woodland border; not a primary inhabitant of evergreen forest at either study site.

White-tipped dove (*Leptotila verreauxi*), 206 grams (W. Shifflet, personal communication).—CORONA: R (5.8 ± 1.2). Foraged on ground, usually in open areas at dawn and dusk; always flew below the canopy and perched below 4 m. Singing increased March through June; nest under construction 2 m high in dense vine tangle 4 m from river, 10 April 1974. GRANDE: LM; 1-2 more adults in June than December-April (3.0 ± 1.5). April (two eggs) and June (two nestlings) nests in dense subcanopy, 1-5 m high. General behavior as at Río Corona.

Green parakeet (*Aratinga holochlora*), 145 grams, N = 5.—CORONA: M; absent December-early March, although present throughout winter 125 kilometers south. Flocks in March and pairs in golden-fronted woodpecker and other cavities, above 7 m, by 8 April 1974, (8.0 ± 2.8). April 1974 nest (eggs?) in river bank cypress; June 1976 nest in ebony 75 m from river had single, feathered juvenile; simultaneously, another pair and single helper tended two feathered nestlings in a natural cypress hole in which all five roosted together (also see elegant trogon).

Red-crowned parrot (*Amazona viridigenalis*) 345 grams, N = 2.—CORONA: LM, especially in December-january (9.3 ± 0.8). Eight in January 1974, 3-10°C, left for two days when air temperatures dropped below freezing. In April, June, most left plots by 1000 hours, returning to roost at 1700-1800 hours, although one or two pairs often stayed. Copulation on 10 April; pairs in natural cypress cavities and those of lineated woodpeckers, 8 April-21 June 1973 and 1976.

Yellow-headed parrot (*Amazona oratrix*), 575 grams, N = 2.—CORONA: LM; like the red-crowned parrot in daily movements and temporary emigration coincident with freezing weather (4.7 ± 0.8). Pair nested in a cypress cavity, June 1976, but by 1978 most suitable cavities had been opened by Mexicans to obtain nestlings for the pet trade and all parrots were scarce. While wary of man and intolerant of red-crowned parrots normally, in April 1974 both species fed in the same ebonies together, dropping opened seed pods on me 3-4 m below.

Yellow-billed cuckoo (*Coccyzus americanus*), 56 grams, N = 13. GRANDE: M. (2.8 ± 0.8); returned in early April. Nests 2 and 3 m high in brasil and anacua (*Ehretia anacua*), respectively, June 1976. Seemingly the subcanopy, insect-foraging equivalent of the squirrel cuckoo. The yellow-billed cuckoo is a passage migrant at the Río Corona.

Squirrel cuckoo (*Piaya cayana*), 100 grams, N = 24.—CORONA: R (2.7 ± 0.9). Possibly absent until 1975 (tentative sighting April 1974). Courtship feeding in June 1976, but nest not discovered. Foraged and drank at the riverbank in a nine-species, passerine and golden-fronted woodpecker flock, January 1975.

Groove-billed ani (*Crotophaga sulcirostris*), 77 grams, N = 20.—CORONA: LM (3.5 ± 1.1); usually absent, December-March but one in January 1975. Five-bird nesting colony in huisache grove at forest-woodland border, June 1973; three in June 1976. One-two active nesets at 2-3 m, not observed closely but seemingly communal (See, Vehrencamp, 1978). GRANDE: LM (1.2 ± 0.5); earliest bird on plot 11 April 1978, but a few usually winter in the region. Unwatched nests below 3 m in huisache and granjeno each June; fledglings in June. Like the white-winged dove in its forest-margin breeding site.

Eastern screech-owl (*Otus asio*), 172 grams, N = 52.—GRANDE: R (1.8 ± 0.5). Called December-June unless repressed by weather or visiting great-horned owls (*Bubo virginianus*). On 19-20 and 23-25 March 1978, at 1800-1930 hours, two territorial pairs contended for a cavity 4 m high in a sugarberry (*Celtis laevigata*), chiefly with descending trills. Elf owls called simultaneously 100-150 m away (screech-elf interactions were rare because elf owls selected thorn woodland or mesquite grassland, whereas screech owls preferred evergreen forest). Pair with two fledglings in June 1976. Curiously absent from Río Corona plots but not found nesting within eight hectares of any *Glaucidium* in my experience.

Ferruginous pygmy-owl (*Glaucidium brasilianum*), 64 grams, N = 23.—CORONA: R (2.5 ± 0.7). Occupied woodpecker holes by late March; on 22 March 1978, two territorial pairs began antiphonal and synchronous calling at 1900 hours with much flying and some screeching within about 900 m^2. At dusk 3-7 June 1973, a pair fed cicada nymphs to at least three feathered nestlings 3 m above ground in an old golden-fronted woodpecker hole in a coma. All observed nesting activity was crepuscular or nocturnal.

Elf owl (*Micrathene whitneyi*), 35 grams, N = 3.—GRANDE: M (0.8 ± 0.7); earliest return 19 March 1978. Primarily outside evergreen forest but nest in one plot near its border, June 1976 (see eastern screech owl). Single bird called there but screech owl drove it away at 1900 hours, 18 April 1975. Nest site a ladder-backed woodpecker hole, 3 m high, in dead anachua limb, 5 m from a noisy water pump and 400 m from the closest screech owl nest.

Mottled owl (*Ciccaba virgata*), 338 grams, N = 14.—CORONA: R (1.3 ± 0.9); one pair in area of both plots. Rarely heard December-March; more often vocal in April and June except during great-horned owl visits. Much shyer than small owls; daytime vocalizations rare. Nest not located.

Common pauraque (*Nictidromus albicollis*), 63 grams, N = 25.—Corona: R (1.3 ± 0.8). Normally silent December-January, sporadic calling in March, frequent April, June. Grande: R (2.2 ± 0.7). One flushed at 1500 hours, 27° C, January; but another January bird appeared torpid with only its back exposed in deep leaf litter at 0900 hours and 6° C. One nesting pair per plot but 1-6 calling individuals per 400 m along a gravel road in late March to June. Pauraques aggregated for lek-type (communal) calling in open areas beginning about 1900 hours in March and 2045 hours June; dispersed in 20-40 minutes and, less frequently, reassembled at dawn.

Buff-bellied hummingbird (*Amazilia yucatanensis*), 4 grams, N = 8.—Corona: LM (1.8 ± 1.3); like the parrots in emigration during severe December-January weather. Present daily March-June; fed in shrub and herb strata, particularly upon Turk's cap (*Malvaviscus drummondii*). Nest not found. Grande: LM (1.2 ± 0.8); as at Río Corona but greater fidelity in winter, possibly because of hummingbird feeders and planted nectar sources nearby. Three unwatched nests, June 1974 and 1976, 2.0-2.5 m high in vine tangles on small trees.

Elegant trogon (*Trogon elegans*), 70 grams, N = 7.—Corona: R (2.5 ± 0.7). Usually silent and solitary December-January; paired and calling March-June. Only twice in 11 mixed, winter flocks of large passerines were trogons associated. Pair excavated old, natural, ebony cavity 8-10 April; pairs in June used lineated woodpecker holes in black willows (*Salix nigra*); 1973 nest two m above river and one m from bank, occupied by nesting green parakeets in June 1976. Two fledglings with male, 23 June 1976.

Blue-crowned motmot (*Momotus momota*), 104 grams, N = 22.—Corona: R (3.3 ± 1.5). Hooting infrequent December-January, common March-June. Not seen in mixed species flocks. Sometimes hover-fed on foliage like elegant trogon. Pair investigated bare riverbank 21-23 March 1978, started to dig burrow 2 m above river on 23rd; another pair dug in man-made dirt bank 2 m above river level and 10 m from it, 9-11 April 1974; a third pair repeatedly investigated the soil pit used by ringed kingfishers but was driven off by them (see below). One-two fledglings with adults in June.

Ringed kingfisher (*Ceryle torquata*), 330 grams, N = 8.—Corona: R (2.8 ± 0.9). Nestlings in burrow 2.5 m from bottom of 6 by 6 by 4 m (deep) soil pit in the forest, 15 m from river, March 1978. Pair dug burrow 3 m above river in natural cutbank, January 1974, but did not nest in January 1975, a more severe winter. Fledglings in April and June. Adults occasionally perched in forest.

Golden-fronted woodpecker (*Melanerpes aurifrons*), 80 grams, N = 28.—Corona: R (4.2 ± 1.2). Adults fed nestlings in ebony snag 3 m high, June 1973, 5 m from old cavity housing ferruginous pygmy owl nestlings.

Fledglings with adults June 1976. GRANDE: LM; like white-tipped dove with breeding seasonal increase (2.3 ± 0.5 in December-March to 5.0 ± 0.8 in June). June pair with nest 5 m high in tepeguaje stub assisted by adult helper; other June nests 1.5 and 3.5 m high in dead tepeguaje and anachua limbs. Fledglings 21 June 1976. As at Río Corona, commonly foraged with green jays, altamira orioles, great kiskadees, and other resident passerines in winter.

Ladder-backed woodpecker (*Picoides scalaris*), 33 grams N = 18.—GRANDE: R (1.8 ± 1.1); mostly peripheral to forest. Nest 2.5 m high in dead mesquite limb at forest-woodland border, June 1976. Solitary winter forager in forest; similar habits but only occasional at Río Corona.

Lineated woodpecker (*Dryocopus lineatus*), 135 grams, N = 13.—CORONA: R (2.0 ± 0); single pair all year in the area of both plots like the mottled owl. Pair fed large nestlings in black willow cavity, 3 m high and 1.5 m from river bank, June 1973; nest only 2 m from active elegant trogon nest in older lineated woodpecker cavity in same clump of willows.

Brown-crested flycather (*Myiarchus tyrannulus*), 38 grams, N = 15.—GRANDE: M (2.3 ± 0.5); first noted 19 March 1978 but none first week of April 1977. Nest in natural and golden-fronted woodpecker cavities, June 1974-1976; pair with single fledgling 18 June 1975. Species appears to be ecological equivalent of sulphur-bellied flycather at Río Corona, where the brown-crested is a passage migrant, at least on my plots.

Great Kiskadee (*Pitangus sulphuratus*), 74 grams, N = 17.—CORONA: R (3.8 ± 0.4). Nest building 21 March-11 April, above 3 m, in Montezuma cypress and ebony; nestlings in June 1973, 2.5 m directly below rose-throated becard nestlings. December-March fruit-eating in forest; 70 percent of time spent along river, although fish-catching infrequent by contrast with the Rio Grande. Foraged with other, large passerines but not inclined to move concurrently with jays, orioles, Couch's kingbirds. GRANDE: LM? (0.8 ± 0.7). A nest, 5 m high in ebony, built first week of April 1977. No observations of fruit-eating and no known interactions with other flycatchers as at Río Corona.

Sulphur-bellied flycatcher (*Myiodynastes luteiventris*), 48 grams, N = 6.—CORONA: M (2.0 ± 0). Absent late December to at least 11 April. Nests above 2 m in Montezuma cypress, black willow and ebony cavities, both woodpecker-drilled and natural, in June; three fledglings with adult pair 21 June 1976.

Couch's kingbird (*Tyrannus couchii*), 39 grams, N = 32.—CORONA: LM; influx in December-April (4.5 ± 3.3) versus June (1.7 ± 0.5). Ten foraged with four other passerines; ate mostly insects, rarely fruit like associated great kiskadees, 23 March 1978. Nests 2-5 m high in eastern cottonwoods (*Populus deltoides*), April 1974 and June each year. GRANDE: LM, outflux December-April (1.3 ± 0.5) versus June (3.3 ±

0.4). Do some individuals of this and other tropical species at their northern limits, like the red-billed pigeon and clay-colored robin, move from the Rio Grande area southward in the winter? More solitary in winter than at Río Corona; used tree canopy and forest interior more frequently than great kiskadee. Nests in a variety of trees, 2-4 m high, late April, June.

Rose-throated becard (*Pachyramphus aglaiae*), 33 grams, N = 23.—CORONA: R (4.2 ± 1.2). Winter mixed foraging with jays, orioles, tanagers. Nesting territories about 150 m apart along river; nests in lower limbs of tepeguaje and cypress, often within a few meters of active altamira oriole and great kiskadee nests, April and June; nestlings in June 1973. GRANDE: LM?; a female made three unsuccessful nesting attempts in dead lower tepeguaje branches, 2.5 m high, April and June 1977. No male seen. By March 1978, house sparrows (*Passer domesticus*) took over the last nest, which then blew down.

Green jay (*Cyanocorax yncas*), 77 grams (D. Gayou, personal communication).—CORONA: R (4.5 ± 3.3). Usually foraged with orioles, tanagers, grosbeaks, kingbirds in December-March; noisiest, most quarrelsome member of such flocks. Nests with eggs (April) and nestlings (June), 3-10 m high, in dense subcanopy trees with vine tangles, attended secretively by more than one pair (see Gayou, 1986). Nested and foraged further from river and foraged less commonly on ground than brown jay. GRANDE: R (4.1 ± 1.4); typically one flock of four or five per plot. Foraged with altamira orioles, Couch's kingbirds, and golden-fronted woodpeckers, December-March, as at Río Corona in canopy and subcanopy, but more frequently on ground at Rio Grande. Courtship in March-April; nesting unobserved.

Brown jay (*Cyanocorax morio*), 206 grams, N = 12.—CORONA: R; usually in monospecific flocks of 4-15, December-March (9.5 ± 3.2). Nest (eggs) in April 1974, attended by five birds; four nestlings fledged 22 June 1976; both nests 11-12 m high in ebony crowns, about 30 centimeters in diameter, built of large twigs and small sticks much like nests of the gray hawk. Courtship feeding in March. On flocking and foraging behavior at the site see Morrison and Slack (1977).

Mexican crow (*Corvus imparatus*), 235 grams, N = 8.—CORONA: R (4.5 ± 2.3). Flocks of three to nine in December-March; paired in April and carrying sticks. Nesting off plots but fledglings present 21-23 June 1976. Foraged almost exclusively on riparian items but in March 1978 ate fruit in forest.

Tufted titmouse (*Parus bicolor*), 22 grams, N = 38.—CORONA: R (3.7 ± 0.8); foraged with migrant warblers, gnatcatchers, kinglets in canopy through winter-early spring; for example, a pair accompanied 36 small passerines of seven species at 0830 hours, 25 March 1978. Courtship in March-April but nesting unobserved; fledglings in June. GRANDE: R (2.2

± 0.9). Two fed with 11 wintering passerines of six species in canopy (70 percent) and subcanopy (30 percent), 21 March; then with a northern house wren (*Troglodytes aedon*), hermit thrush (*Catharus guttatus*), and pair of long-billed thrashers (*Toxostoma longirostre*), they mobbed a calling eastern screen owl at 1700 hours. Nesting 1.5 m high in dead anacua, old woodpecker hole, April 1977.

Spot-breasted wren (*Tryothorus maculipectus*), 16 grams N = 22.—CORONA: R (5.3 ± 0.9). Singing birds year-round, at least 100 m apart in about 50 m-diameter territories centered on dense shrubs in clearings and plot edges. Only once seen foraging in a mixed passerine flock of warblers, wrens, and sparrows in these same thickets in winter. Apparent niche equivalent of Carolina wren at Rio Grande but much shyer; nests unobserved.

Carolina wren (*Thryothorus ludovicianus*), 19 grams, N = 16.—GRANDE: R (1.2 ± 0.7). Solitary or paired with year-long territory in subcanopy positions like spot-breasted wren. Nest (eggs?) in rotten stump of Berlandier ash (*Fraxinus berlandierana*), April 1977.

Clay-colored robin (*Turdus grayi*), 76`grams,N = 23.—CORONA: LM; December-March influx (4.3 ± 1.5) versus single pair in June (2.0 ± 0). Nestlings June 1973, 3.5 m high in subcanopy brasil; fledglings June 1976. Winter flocks with large resident passerines plus occasional squirrel cuckoos and golden-fronted woodpeckers; three amongst 26 birds of seven species in canopy (61 percent) and subcanopy (39 percent) strata, 1 January 1975. Occasional singing March, frequent in April and June. GRANDE: one on both plots December-June 1978.

Yellow-green vireo (*Vireo flavoviridis*) 19 grams, N = 11.—CORONA: M; one pair with nestlings, 3 m high in a 4 m pata de vaca (*Bauhinia divaricata*) 10 m from river, 3-7 June 1973, but apparently not in the plots thereafter.

Tropical parula (*Parula pitiayumi*), 8 grams, N = 7.—CORONA: LM; December-January outflux (2.2 ± 0.2) compared to March-June (5.3 ± 1.6) when nested in ballmoss (*Tillandsia recurvata*) above 10 m in riverside trees; two nests (eggs?) 350 m apart, April 1974. Flocked with migrant canopy-users, chiefly warblers, gnatcatchers, and kinglets, December-March, when more numerous than the wintering northern parula (*P. americana*).

Grimson-collared grosbeak (*Rhodothraupis celaeno*), 50 grams, N = 2.—CORONA: LM; December-April (1.5 ± 0.7). One accompanied a 26 bird flock, 1 January 1975 (see clay-colored robin); regular in winter censuses. A pair with two fledglings nested in forest immediately outside one plot, June 1973, but not noted otherwise in June. Increasing disturbance by campesinos, hunting, and wood-cutting, may have been a factor with this and other species like the yellow-green vireo.

Blue bunting (*Cyanocompsa parellina*), 16 grams, N = 20. CORONA: R (2.0 ± 1.2). Occupied shrub thickets of forest clearings; rarely at river or roadside hence somewhat segregated from olive sparrow and spot-breasted wren. Territorial males no closer than about 30 m from territorial olive sparrows. Mottled and blue males sang in March-June; nests unobserved. Occasionally entered winter, ground-shrub foraging flocks; for example a male accompanied nine, small, migrant passerines, 18 March 1978 (see below).

Olive sparrow (*Arremonops rufivirgatus*), 24 grams, N = 19.—CORONA: R (6.8 ± 1.2). Foraged with Lincoln's sparrow (*Melospiza lincolnii*) in winter and white-tipped dove year-round (70 percent time on ground versus 50 percent on ground in blue bunting and northern cardinal, *Cardinalis cardinalis*); song perches to two m in dense shrubs. GRANDE: LM: December-January outflux (1.7 ± 0.9) compared to April, June (4.7 ± 0.9). Habits as at Río Corona; nests unobserved at both sites.

Bronzed cowbird (*Molothrus aeneus*), 54 grams, N = 31.—CORONA: LM; usually absent December-March but common April, June (6.5 ± 2.5), when "helicopter hovering" courtship of males frequent in man-made clearings. GRANDE: LM; like Río Corona but notably less abundant (4.0 ± 0.8). A female repeatedly tried to enter an altamira oriole nest under construction, 11 April 1974, but was repulsed by the pair.

Hooded oriole (*Icterus cucullatus*), 25 grams, N = 8.—CORONA: R (2.7 ± 0.9). Usually flocked with altamira orioles and similar large passerines in tree canopy December-March, although a pair foraged with Lincoln's sparrows, northern house wrens, and orange-crowned warblers (*Vermirora celata*) in 1-2 m shrubs, March 1978. Nestlings 12 m high in ebony, 300 m from the river, June 1973. GRANDE: R; common in late 1950's, scarcer in 1960's, and absent during this study (Gehlbach, 1981:25).

Altamira oriole (*Icterus gularis*), 67 grams, N = 25.—CORONA: R (6.0 ± 2.2). Core member of larger passerine flocks in winter, but monospecific flock of 21 on 22 March 1978. Persistent singing in March, nest-building 9-11 April and 3-7 June at about 100 m intervals along river in drooping cypress and tepeguaje branches at least 5 m high. GRANDE: LM; December-March outflux (0.8 ± 0.8) versus April, June (2.2 ± 0.9). Nestlings 6.5 m high in tepeguaje, June 1976; nest building in April (see bronzed cowbird). Winter flocks with other large passerines cover 1.5-3.5 times more lineal area/time than at Río Corona, suggesting scarcer food at this marginal northern locale.

Audubon's oriole (*Icterus graduacauda*), 46 grams, N = 20.—CORONA: R (2.5 ± 0.8). In winter flocks less frequently than other orioles (27 percent of flocks versus 73 percent average for hooded and altamira, N = 11). April and June birds usually stayed 50 m or more from river as did hooded orioles, compared to river-nesting altamira orioles; sang year-round like congeners, suggesting permanent territory; nest unobserved.

TABLE 1. Biomass and density of breeding birds (excluding ducks and kingfishers) in riparian evergreen forests of the Río Corona and Rio Grande, 1973-1978, and concurrent, monthly climatic means plus or minus one standard deviation from Victoria, Tamaulipas (Río Corona), and McAllen, Texas (Rio Grande).

Seasons	Parameters	Río Corona	Rio Grande
Winter (December-March)	Biomass (kg/ha)	2.8	0.9
	% nonpasserine	76.4	92.4
	$\bar{x} \pm$ SD/species (g/ha)[1]	94.2 ± 140.4	75.2 ± 200.6
	Density (n/ha)	16.1	4.2
	% nonpasserine	47.0	64.1
	$\bar{x} \pm$ SD/species[2]	0.5 ± 0.3	0.3 ± 0.3
Breeding (April-June)	Biomass (kg/ha)	2.8	1.2
	% nonpasserine	80.6	87.5
	$\bar{x} \pm$ SD/species (g/ha)	80.9 ± 125.9	52.9 ± 155.3
	Density (n/ha)	17.8	7.2
	% nonpasserine	51.8	55.9
	$\bar{x} \pm$ SD/species (g/ha)	0.5 ± 0.3	0.3 ± 0.2
Dry (November-April)	Temperature (°C)	20.0 ± 1.1	19.1 ± 1.2
	Precipitation (cm)	3.1 ± 0.3	2.9 ± 0.4
Wet (May-October)	Temperature(°C)	26.2 ± 0.8	28.5 ± 0.7
	Precipitation (cm)[3]	12.3 ± 1.3	5.0 ± 0.6

[1] Inter-site biomass comparisons insignificant in winter and breeding seasons ($P > 0.05$); species = 30 (Corona) versus 13 (Grande) and 35 versus 22, respectively.

[2] Inter-site density comparisons signficant in winter ($F = 3.9$, $P = 0.05$) and breeding ($F = 5.2$, $P = 0.02$) seasons.

[3] Only significantly different climatic feature ($F = 15.3$, $P = 0.01$).

GRANDE: R; one pair on territory in cedar elms (*Ulmus crassifolia*), hung with spanish moss (*Tillandsia usneoides*), January-June 1976; nest unobserved. No other records from study plots. Much rarer in 1970's than earlier (Gehlbach, 1981:25).

BIOMASS, DENSITY, AND CLIMATE

The Río Corona forest supported 2.3 (breeding season) to 3.1 (winter) times more avian biomass per unit area with 2.5 (breeding) to 3.8 (winter) times higher density of breeding birds than the Rio Grande forest (Table 1). Interestingly, nonpasserine species are relatively more important at the Rio Grande, despite that fact that they are usually considered to be so in the tropics. Nevertheless, they dominate both avifaunas. Birds at the Rio Grande are no larger on average, but they are less dense and more variable in both density and biomass per species than at the Río Corona. Of particular interest is the 2.7 times overall increase in biomass at the Río Corona; because it corresponds closely to 2.5 times greater wet-season rainfall, the only major climatic feature that differs between the two locales (Table 1).

Earlier, I postulated that more precipitation is the key to understanding increased food production and hence avifaunal diversity at the Río Corona (Gehlbach et al., 1976). Subsequently, I also suggested that added rainfall, especially in the nesting season, explains the general regional increase in nonpasserines; because it enhances food-type diversity as well as productivity, which permits more nonpasserines to coexist. Conversely, passerines are more strongly separated by topographic diversity,which is minimal in the Rio-Grande-Río Corona lowlands (Gehlbach, 1987). Thus, despite their considerable thermal, vegetative, and bird-species similarities, the Río Corona avifaunal is richer and more productive than its Rio Grande counterpart.

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CLEAR FORK VERTEBRATES AND ENVIRONMENTS FROM THE LOWER PERMIAN OF NORTH-CENTRAL TEXAS

Phillip A. Murry and Gary D. Johnson
Tarleton State University, Stephenville, Texas 76402, and
University of South Dakota, Vermillion, South Dakota, 57069

Abstract.—Vertebrate fossils were collected from the Arroyo, Vale, and Choza formations of the Clear Fork Group (early Permian) in north-central Texas. The Arroyo, lowest of the three Clear Fork units, yielded the most diverse vertebrate faunas. In the lowermost Arroyo, rare occurrences of fusulinids and certain sharks indicate a marine influence. In the youngest beds of the lower Arroyo, the shark *Xenacanthus* disappears, but other taxa such as the lungfish *Gnathorhiza*, the amphibian *Lysorophus*, and terrestrial amphibians and reptiles increase in abundance and diversity. By middle Arroyo deposits, this condition is reversed and the assemblages become dominated by *Orthacanthus* or *Diplocaulus*. This suggests that environmental conditions, or at least preservational factors, had deteriorated. Except for one locality in the lower Vale, faunal abundance continues to decrease and both faunal diversity and abundance further decline above middle Vale deposits. Although environmental factors were probably in part responsible for the decline with initiation of sabkha conditions, preservational factors also played a role in the decrease of relative faunal abundance in the Vale and Choza units. Influences on the environment would have included eustatic changes in sea level related to basin subsidence and Gondwanaland glaciation, possible fluctuations in the intertropical convergence zone, and orographic effects. *Key words*: Texas geology; Lower Permian, Clear Fork Group; vertebrate paleontology; paleoecology.

The Clear Fork Group (Permian, Leonardian) is traditionally divided into three formations. In ascending order these are the Arroyo, Vale, and Choza. To the south of the study area these formations are separated by the Standpipe Limestone at the top of the Arroyo Formation and the Bullwagon Dolomite at the top of the Vale Formation (Olson, 1958). However, in north-central Texas there are no marine marker beds by which the terrestrial Clear Fork facies may be separated. The objective of this study was to document changes in vertebrate abundance and diversity throughout the Clear Fork Group in the vicinity of the Wichita River in north-central Texas (Fig. 1). Because there are no marker beds to differentiate the Clear Fork Group in north-central Texas and the lithologies are not distinct enough to distinguish the three formations as separate mappable units, the beds above the Lueders Limestone and below the unconformity with the San Angelo Formation are regarded as undifferentiated Clear Fork units. The fossils recovered reveal significant changes through this portion of the section, but no biostratigraphic zones could be delineated. Using E. C. Olson's (1951a, 1951b, 1952a, 1952b, 1954, 1955a, 1955b, 1956, 1958) interpretations of this part of the Clear Fork as a guide, we grouped our localities into corresponding Arroyo, Vale, and Choza categories for comparative purposes.

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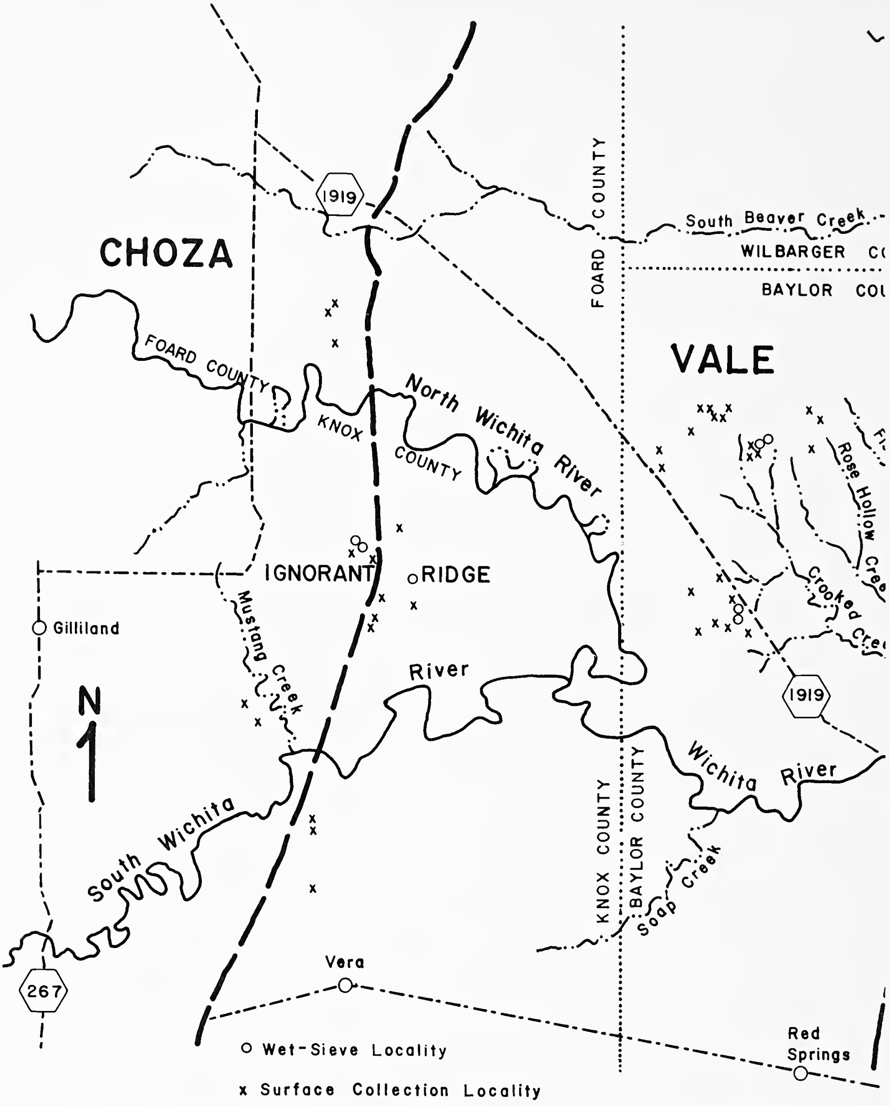

FIGURE 1. Distribution of vertebrate fossil localities in the Clear Fork Group.

Surface collections of vertebrate fossils were made at 94 sites. About 20 percent of the localities yielded microvertebrates, obtained by bulk-sampling methods such as wet-sieving. Many taxa of fishes and tetrapods were recovered (Table 1), which constitute a larger and more diverse sample size than could possibly have been obtained by standard collecting procedures. In cases where articulated specimens were discovered, excavation by standard quarrying techniques was carried out.

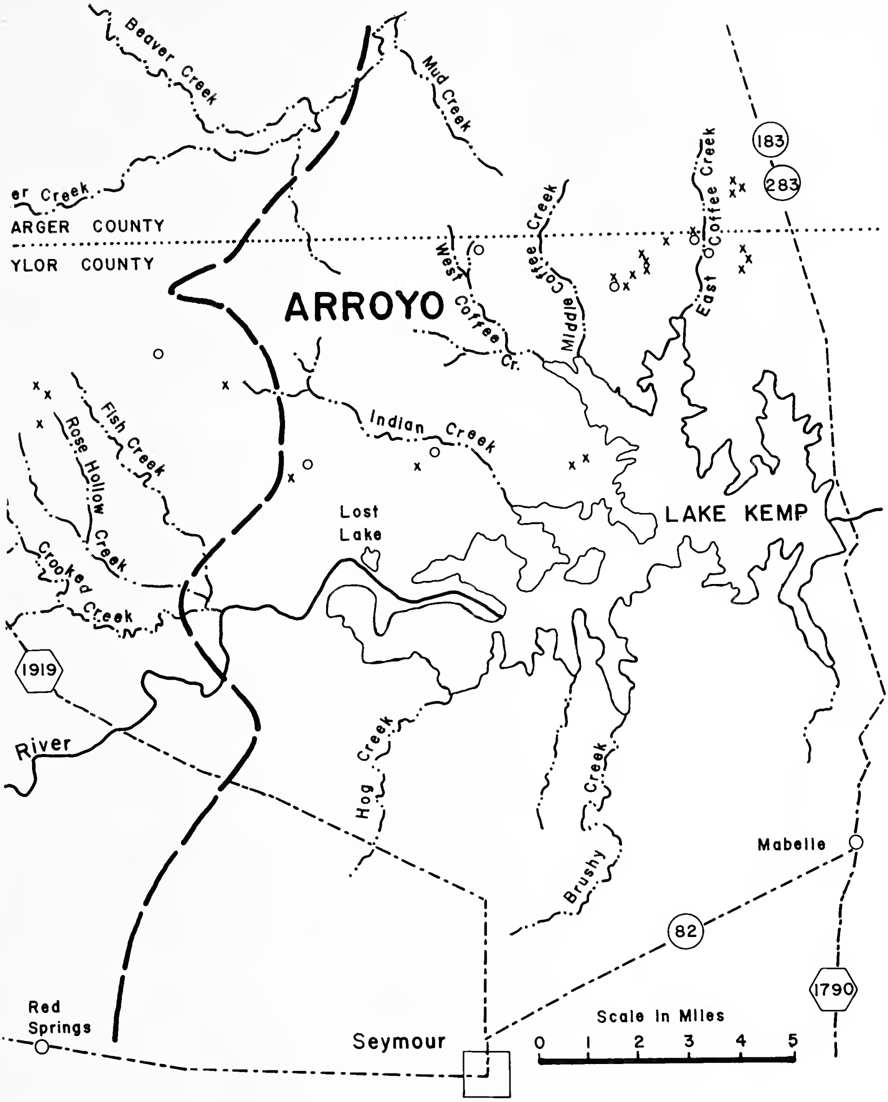

FIGURE 1. Continued.

Thousands of macrovertebrate and microvertebrate fossils were collected, and serve as the basis of this study (Appendix).

LOWER ARROYO FAUNAS AND ENVIRONMENTS

The Arroyo unit (in the lower Clear Fork beds) contains the most prolific fossil localities in both faunal diversity and abundance. Our observations of the middle and upper lithologies of the Arroyo in the

TABLE 1. Vertebrates identified from the Clear Fork Group.

- Class Chondrichthyes
  - Subclass Elasmobranchii
    - Order Xenacanthodii
      - *Xenacanthus luedersensis*
      - *Orthacanthus platypternus*
    - Order Chimaerida
      - *Helodus*?
- Class Osteichthyes
  - Subclass Actinopterygii
    - Order Palaeoniscida
      - indeterminate paleoniscoids
  - Subclass Dipnoi
      - *Gnathorhiza* sp.
      - *G. dikeloda*
- Class Amphibia
  - Subclass Labyrinthodontia
    - Order Temnospondyli
      - *Trimerorhachis* sp.
      - *Eryops* sp.
      - *Zatrachys*?
    - Order Anthracosauria
      - *Cricotus*?
      - *Seymouria* sp.
      - *Waggoneria*?
      - *Diadectes* sp.
      - indeterminate seymouriamorphs
  - Subclass Leposondyli
    - Order Nectridea
      - *Diplocaulus* sp.
    - Order Microsauria
      - *Lysorophus* sp.
      - *Euryodus* sp.
      - *Ostodolepis* sp.
      - indeterminate microsaurs
- Class Reptilia
  - Subclass Anapsida
    - Order Cotylosauria
      - *Captorhinus* sp.
      - *Labidosaurus* sp.
      - indeterminate large captorhinomorph
  - Subclass Euryapsida
    - Order Araeoscelida
      - araeoscilid?
  - Subclass Synapsida
    - Order Pelycosauria
      - *Varanops*?
      - *Dimetrodon* sp.
      - *Edaphosaurus* cf. *E. pogonias*
      - indeterminate caseid

Indian Creek, West Coffee Creek, and Lost Lake areas agree with Olson's (1958) description as "even red shales" (silty mudstones).

Lowermost Arroyo

The lower Arroyo unit in the East Coffee Creek area is lithologically more variable than noted in previous studies. Some beds in this unit consist of rather uniform, dark, reddish-brown mudstone devoid of recognizable sedimentary structures. However, the most prolific localities occur in reddish-brown, clay-pebble conglomerates or silty mudstones, which underlie light green siltstone. This lithologic diversity within a restricted stratigraphic horizon indicates significant variations in depositional environment.

The area may have been a coastal plain during local Arroyo deposition as there appears to be some marine influence. Only three fusulinid foraminifers were recovered from the lower part of the Arroyo unit; however, they may not have been reworked from earlier deposits. No fusulinids were recovered from the Wichita-Albany Group in north-central Texas using similar collection techniques (Johnson, 1979: appendix).

A major difference between the Clear Fork Group and the underlying marine/nonmarine Wichita-Albany Group (Johnson, 1981) is the sparseness of shark remains in the Clear Fork. Only three helodont shark teeth were recovered from the Clear Fork; all came from the lower portion of the Arroyo. These teeth may have been reworked from the Wichita-Albany Group, although the presence of a euryhaline helodont shark cannot be discounted. In the Wichita-Albany, helodont sharks represent approximately one percent of the total chondrichthyan assemblage (Johnson, 1981: fig. 3). The most common sharks in the Wichita-Albany include *Orthacanthus texensis* and *Xenacanthus luedersensis.* With the exception of 40 abnormally large *X. luedersensis* teeth collected from the lower Arroyo, neither of these taxa appear in the Clear Fork Group. Some sharks may have been freshwater or euryhaline during Wichita-Albany time, but their near absence in the Clear Fork suggests they were marine. The abnormal *X. luedersensis* teeth, sparse fusulinids and helodonts, and the absence of other chondrichthyans indicate that the typical Wichita-Albany marine environment is not represented in the lower Clear Fork.

The xenacanthodiids, traditionally considered as freshwater sharks, further complicate the pattern. The most common, presumably freshwater shark in the Wichita-Albany, *Orthacanthus texensis*, is entirely absent from the Clear Fork. *Xenacanthus luedersensis*, the second most common shark in the Wichita-Albany, is fairly common in the lowest part of the Arroyo; it is absent throughout the remaining Clear Fork. Only *Orthacanthus platypternus*, which appears throughout the Wichita-Albany, persists throughout the Clear Fork, often as the most common fossil.

Our studies show that the lowest part of the Arroyo in the East Coffee Creek area exhibits more diversity than previously reported. The last (youngest) positively identified remains recovered in this study of *Edaphosaurus*, a single specimen of an embolomere, and *Zatrachys*-like elements may represent relict survivors of the older Wichita-Albany fauna. However, well-documented remains of *Edaphosaurus pogonias* have been recovered from areas west of Middle Coffee Creek and some fragments have been found in West Coffee Creek (E. C. Olson, personal communication), although the absence of this taxon in our collections from this area probably demonstrate it's rarity in the Clear Fork Group.

Middle Lower Arroyo

The middle portion of the lower Arroyo contains numerous localities in the East Coffee Creek area and these are the most prolific in the Clear Fork Group. Taxa include xenacanth sharks and lungfish; amphibians, including seymouriamorphs, diadectids, *Diplocaulus*, *Lysorophus*, and microsaurs; and reptiles, such as captorhinids and pelycosaurs. Although similar in general faunal representation, these assemblages exhibit more diversity than should be expected. The stratigraphically lowest of these assemblages (locality 37; see Appendix) consists mostly of *Orthacanthus* (*O. platypternus*) teeth. This assemblage occurs in a cross-laminated, clay-pebble conglomerate, representing a channel deposit. Within localities adjacent to locality 37 but that are probably slightly higher stratigraphically, diversity decreases, and there is an extreme decrease in numbers of *Orthacanthus* teeth. These assemblages are from reddish-brown mudstones, which represent overbank and pond deposits in which large xenacanth sharks (*Orthacanthus*) would not be present, but a wide variety of other smaller taxa could be found. The number of *Diplocaulus* specimens increases compared to the xenacanths in these deposits. Diversity decreases in most of these overbank deposits to the point where only isolated remains of *Diplocaulus* and *Dimetrodon* are found.

Upper Lower Arroyo

There is a major change in the general faunal composition in the youngest beds of the East Coffee Creek area. This is illustrated at locality 47. The last *Xenacanthus* teeth occur in these beds; although there is a major decrease in the number of *Orthacanthus* teeth, they still constitute about 20 percent of the identified material. The number of *Gnathorhiza* elements, the only lungfish genus recovered from all Clear Fork units, increases dramatically. No locality lower in the section contains more than eight percent lungfish elements, whereas *Gnathorhiza* tooth plates in these beds constitute about one-third of the identified elements. Locality 47 is one of only two assemblages in the Clear Fork Group where palaeoniscoid elements are numerous. There is also a large increase in the relative abundance of *Diplocaulus* at this horizon, but presumed terrestrial components such as microsaurs, seymouriamorphs, captorhinomorphs, and pelycosaurs maintain about the same relative abundance as in lower deposits. This assemblage is unlike the older Arroyo assemblages, with a much lower percentage of *Orthacanthus* relative to *Gnathorhiza* and a higher percentage of *Diplocaulus*. Seasonality may have increased during this period inasmuch as the first large concentrations of *Lysorophus*, an aestivating amphibian, occur at locality 48. This complements the large increase in *Gnathorhiza*, a known aestivator since Wichita-Albany time (Berman, 1976).

Middle and Upper Arroyo Faunas and Environments

By middle Arroyo time, there is a large decrease in vertebrate diversity and abundance. Locality 52 in the lower portion of the middle Arroyo unit contains a moderately diverse assemblage, including *Orthacanthus*, *Diplocaulus*, microsaurs, captorhinids, and *Dimetrodon*, but numbers of recovered elements are much lower than from the lower Arroyo. The lithology of most middle Arroyo localities consists of reddish-brown mudstone. The only other locality with moderate diversity (locality 56) is covered by a calcareous lag gravel, which differentiates it from other middle Arroyo sites. A large number of *Orthacanthus* teeth were recovered from this locality, as well as palaeoniscoid fish scales, *Diplocaulus* and *Dimetrodon*.

It seems apparent that by middle Arroyo time, environmental conditions, or at least preservational conditions, had deteriorated. However, if seasonality differences were accentuated at this time, we found no evidence of it in the assemblages of the middle and upper Arroyo. Despite intensive searching, no *Lysorophus* localities were found in this portion of the section, and only a few *Gnathorhiza* tooth plate fragments were found in the upper Arroyo. Instead, the faunas are dominated by *Orthacanthus* and *Diplocaulus*, neither of which is believed to have been able to withstand extreme seasonality. Above late Arroyo deposits, *Orthacanthus* and *Diplocaulus* remain the dominant components in the Clear Fork, although their abundance tends to be inversely proportional to each other. This may indicate a preference for deeper streams for *Orthacanthus* and shallower streams or ponds for *Diplocaulus*, but supporting lithologic evidence is inconclusive.

VALE AND CHOZA FAUNAS AND ENVIRONMENTS

The lithology of our lower Vale localities consists primarily of structureless mudstone, thereby differing from the conglomerates described by Olson (1971). However, these apparent lithologic differences may be due to the placement of the tenuous Arroyo-Vale boundary. In lower Vale deposits, there may be some indication of wet-dry seasonality, evidenced by a large concentration of *Lysorophus* nodules in the Rose Hollow Creek area at locality 67. Some lower Vale localities produced a few lungfish toothplates but most yielded either *Orthacanthus* or *Diplocaulus*. A substantial fauna, consisting of numerous *Diplocaulus* skeletons, along with *Orthacanthus, Labidosaurus*, *Dimetrodon*, and caseid pelycosaur remains, occurs in laminated silts and shales at locality 72, which do not indicate wet-dry seasonality. Other than the relatively scarce *Lysorophus* localities, there is little indication of wet-dry seasonality in the lower to middle Vale. *Lysorophus* localities are typically isolated occurrences; although rich in numbers of nodules, the localities reported in this study contain few or no associated taxa. Therefore, the presence of *Lysorophus* suggests adaptation to, or preservation in, unique environments on the floodplain, in which few other species lived or could be preserved, in addition to wet-dry seasonality. However, E. C. Olson (personal communication) reports that *Lysorophus*, *Gnathorhiza*, and *Diplocaulus* may be associated in nodules and burrows. It is his interpretation that they do occur together where there is strong seasonality or aestivation, at least during their early ontogeny. Therefore, the ecological interrelationships of these taxa are not apparent.

The last relatively numerous fossils of any taxon in the Clear Fork Group are preserved in the middle Vale unit at localities 80 and 81. These remains consist almost entirely of *Orthacanthus* teeth, with a few associated elements of palaeoniscoid fish, lungfish, *Diplocaulus*, microsaurs, *Captorhinus*, and *Dimetrodon*. The deposits containing these taxa occur at localities that are different from other, less prolific, middle Vale localities. The lithology consists of clay-pebble conglomerate rather than mudstones, probably representing fluvial deposits. Olson (1971) believed the presence of clay-pebble conglomerates in the middle Vale indicated the initiation of "monsoonal-type rainfall." However, we found the presence of this facies in the middle Vale to be a relatively uncommon occurrence, although our best fossil localities in this unit are associated with it. The lower Arroyo unit contains more widely distributed clay-pebble conglomerates. However, Olson (1971:649) inferred moderate, evenly distributed rainfall throughout the year during lower Arroyo time.

Abundant evaporite minerals occur in the Clear Fork Group for the first time in the middle Vale unit. From upper Vale through Choza deposits, there is an increase in the amount of evaporites, and at several localities there is textural evidence of ground-water influence on evaporite formation and dissolution. The upper Vale and Choza units contain a paucity of vertebrate remains, consisting primarily of *Orthacanthus* and *Diplocaulus*. These taxa often occur in inversely different proportions for any given locality, but the numbers of each may be too meager to be conclusive. We recovered a partial skull of a large captorhinomorph from the upper Vale at locality 89, and a relatively intact skeleton of probably the same taxon was found at locality 96. These large captorhinomorphs are uncommon, and appear to be restricted to the Vale and lower Choza.

As the amount of the evaporites continued to increase, probably indicating more influence from marginal coastal sabkha environments (Smith, 1976), the deposits markedly decrease in both numbers of specimens and in diversity. Despite intensive searching, we did not find any localities above the lower Choza. Presumably, deteriorating environmental factors limited faunal distribution and affected preservation during much of later Clear Fork time.

Discussion

The environmental changes that occurred during Clear Fork time may be related to one or more contemporary events. The general changes in facies from lower to upper Clear Fork are related to basin subsidence in which sabkha conditions were initiated during upper Clear Fork times.

Variance in seasonality (cyclicity), which accompanied this basin subsidence, may have been due to glacially caused eustatic changes in sea level (Presley and McGillis, 1982). Because this region was less than 20 degrees from the equator (Ziegler et al., 1977), local aridity would not have been related to the subtropical high pressure belt associated with latitudes of 20 to 30 degrees. Therefore, the climatic changes observed might be related to variations in the intertropical convergence zone, which probably controlled wet-dry seasonality. Continental effects, interrelationships of atmospheric circulation, and physical barriers, as well as eustatic sea level changes affecting oceanic circulation during glacial episodes, would have influenced both the depositional environments and the distribution of fossil vertebrates in the Clear Fork.

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APPENDIX

CLEAR FORK GROUP LOCALITIES IN APPROXIMATE STRATIGRAPHIC ORDER

Each locality is listed by Southern Methodist University vertebrate locality number, followed by faunal description. Most taxa were identified on the basis of isolated elements. Major faunal descriptions are preceded by a description of the associated unweathered sedimentary facies (color notations are from the Geological Society of America Rock-Color Chart). Sample size for bulk processing is stated in pounds. Formation names are used in an informal sense (based on Olson, 1958) and are not meant to imply differentiation of the Clear Fork Group. All specimens, copies of field sketches, and precise locality data are reposited in the Shuler Museum of Paleontology at Southern Methodist University, Dallas, Texas. Several localities containing as yet unidentified fossils have not been assigned locality numbers, but are on file in the Shuler Museum.

LOWER ARROYO FORMATION

East Coffee Creek area

SMU 33	*Edaphosaurus* cf. *E. pogonias.*
SMU 34	pelycosaur.
SMU 35	small *Diplocaulus* skull and jaws plus associated fragments.
SMU 36	80 lbs.; fusulinids; *Spirorbis*; *O. platypternus*; *X. luedersensis*; *Gnathorhiza*; *Diplocaulus*; amphibian scutes; *Dimetrodon*; coprolites.
SMU 37	Moderate reddish-brown (10R 4/6), calcareous, cross-laminated siltstone with silt pebbles ("clay-pebble conglomerate"). Occurs immediately below light greenish-gray (5G 8/1), noncalcareous, cross-laminated flaggy siltstone. 2200 lbs.; *Spirorbis*; *O. platypternus*; *X. luedersensis*; xenacanth spine fragments and denticles, *Helodus*?; *Gnathorhiza*; palaeoniscoid scales; *Diadectes*; *Diplocaulus*; *Lysorophus*; *Euryodus* (partial skull); unidentified microsaurs; *Captorhinus*; *Labidosaurus*; *Dimetrodon.*
SMU 38	80 lbs.; fusulinid; *O. platypternus*; palaeoniscoids; *Trimerorhachis* (small partial skull and jaws).
SMU 39	Dark reddish-brown (10R 3/4), noncalcareous, slightly silty mudstone with less than one percent light green noncalcareous mudstone. 2000 lbs.; *O. platypternus*,

xenacanth? spine fragments; *Gnathorhiza*; unidentified fish-like centrum; *Trimerorhachis*; *Eryops*; *Zatrachys*?; *Diadectes*; *Seymouria*; *Diplocaulus*; *Lysorophus*; microsaur?; *Labidosaurus*?; *Dimetrodon*; *Varanops*?

SMU 40 xenacanth? spine fragment; large fish? vertebra; *Trimerorhachis*; *Eryops*; *Diadectes*?; *Diplocaulus*; microsaur?; *Labidosaurus*; *Dimetrodon*.

SMU 41 *Diadectes*; small pelycosaur.

SMU 42 *Diplocaulus*.

SMU 43 *Diplocaulus*; *Dimetrodon*.

SMU 44 *Diplocaulus*; *Dimetrodon*.

SMU 45 *O. platypternus*; xenacanth calcified cartilage; *Dimetrodon*.

SMU 46 *Eryops*; *Dimetrodon*.

SMU 47 Pale reddish-brown (10R 5/4) to dark reddish-brown (10R 3/4), calcareous, muddy siltstone. Occurs immediately below a light greenish-gray (5G 8/1), noncalcareous, cross-laminated, flaggy siltstone. 2750 lbs.; *X. leudersensis*; *O. platypternus*; xenacanth calcified cartilage; *Gnathorhiza* (more than one species?); unidentified lungfish?; palaeoniscoid scales; *Trimerorhachis, Cricotus*?; *Waggoneria*?; small seymouriamorph; *Diplocaulus*; *Lysorophus*; *Ostodolepis*; *Euryodus*; unidentified microsaur; *Captorhinus*; araeoscelid?; *Dimetrodon*; *Varanops*?; small captorhinomorph trackway.

SMU 48 *Lysorophus* nodules.

SMU 49 *Diplocaulus*.

SE of mouth of West Coffee Creek

SMU 50 *O. platypternus*; *Trimerorhachis*; small seymouriamorph; *Diplocaulus*; *Dimetrodon*.

MIDDLE ARROYO FORMATION

Indian Creek area

SMU 51 60 lbs. from three horizons; seed?; *Trimerorhachis*?; *Diplocaulus*; *Dimetrodon*.

SMU 52 1200 lbs. from six horizons; *O. platypternus*; xenacanth? spine fragment; palaeoniscoid scale; *Trimerorhachis*?; labyrinthodont; *Diplocaulus*; microsaur?; captorhinid; *Dimetrodon*.

SMU 53 *Diplocaulus*.

SMU 54 *Dimetrodon*.

SMU 55 *Diplocaulus*; *Dimetrodon*.

West Coffee Creek area

SMU 56 Moderate reddish-brown (10R 4/6) to dark reddish-brown (10R 3/4), noncalcareous, slightly silty mudstone; covered by a calcareous lag gravel. 1400 lbs.; *O. platypternus*; xenacanth calcified cartilage; palaeoniscoid scales; *Diplocaulus*; *Dimetrodon*; coprolites.

UPPER ARROYO FORMATION

Area northwest of Lost Lake

SMU 57 Dark reddish-brown (10R 3/4), noncalcareous, silty mudstone that contains light greenish-gray (5G 8/1) irregular spots. Covered (upslope) by fissile to flaggy red siltstone with greenish-gray irregular spots. 500 lbs.; *O. platypternus*; xenacanth calcified cartilage and denticles; broken palaeoniscoid scales (common); *Gnathorhiza*; *Diplocaulus*; *Dimetrodon*; coprolite.

SMU 58 Large pelycosaur bones.

Lowermost Vale Formation (Olson, 1958)

Fish Creek area

SMU 59	Grayish-red (10R 4/2) silty mudstone to siltstone with irregular light greenish-gray (5G 8/1) spots; overlies a light greenish-gray clay-pebble conglomerate. All occur in large-scale cross beds. 500 lbs.; *O. platypternus*; indeterminate bones and teeth.
SMU 60	Grayish-red to reddish-brown siltstone with coarse sand-size clay clasts ("clay-pebble conglomerate"); overlain by pale green muddy siltstone. All occur in large-scale cross-beds; 40 meters across; same as SMU 59, but stratigraphically higher; 250 lbs.; *O. platypternus*; *Gnathorhiza*.
SMU 61	500 lbs.; *O. platypternus*; *Gnathorhiza*; lungfish? scale; *Eryops*; *Diplocaulus*; *Dimetrodon*; coprolites.

Lower Vale Formation

Fish Creek area

SMU 62	Calcified xenacanth cartilage; pelycosaur?
SMU 63	*O. platypternus*; xenacanth calcified cartilage; *Gnathorhiza dikeloda*; *Diplocaulus*; small reptile?

Rose Hollow Creek area

SMU 64	Indeterminate reptile.
SMU 65	*O. platypternus*; *Diplocaulus*; indeterminate bones of large reptile.
SMU 66	*Captorhinus*; large indeterminate fragments.
SMU 67	Lag deposit (15 by 35 meters) of noncalcareous nodules weathering from dark reddish-brown (10R 3/4), calcareous siltstone, which is about 40 centimeters thick. Underlain by dark reddish-brown, blocky, silty mudstone mottled with irregular greenish-gray (5GY 6/1) spots. 1200 lbs. (surface only); *O. platypternus* (three teeth); *Gnathorhiza* (one pterygoid tooth plate, fragments); *Lysorophus* (about 11,300 nodules, 1484 vertebrae).
SMU 68	*O. platypternus*.

Crooked Creek area (southwest)

SMU 69	Partial pelycosaur limb bone.
SMU 70	Moderate reddish-brown (10R 4/6) slightly silty mudstone with irregular light greenish-gray (5GY 8/1) spots. 2000 lbs.; *O. platypternus*; xenacanth calcified cartilage, xenacanth denticle; *Gnathorhiza*, fish scale?; *Trimerorhachis*; *Seymouria*; *Diplocaulus*; pelycosaur; unidentified jaw in plaster jacket; coprolites.
SMU 71	*Diplocaulus*?
SMU 72	Pale reddish-brown (10R 5/4), with some moderate reddish-brown (10R 4/6) and less moderate reddish-orange (10R 6/6), noncalcareous, cross-laminated, muddy siltstone, mottled with very light gray (N8). Contains some light greenish-gray (5G 8/1) laminae. 900 lbs.; *O. platypternus*; seymouriamorph?; *Diplocaulus*; *Dimetrodon*; caseid; also a *Diplocaulus* bone bed currently being excavated.
SMU 73	*Diplocaulus*.
SMU 74	*Diplocaulus*; pelycosaur.
SMU 75	*Diplocaulus*.
SMU 76	*Diplocaulus*.
SMU 77	*Diplocaulus*.
SMU 78	*Diplocaulus*.
SMU 79	*O. platypternus*; labyrinthodont; *Diplocaulus*.

MIDDLE VALE FORMATION

Crooked Creek area (northwest)

SMU 80	Very pale green (10G 8/2) to pale green (5G 7/2) to light greenish-gray (5G 8/1), slightly calcareous mudstone dominated by clay clasts ("clay-pebble conglomerate"). Most of the clasts, together with enclosed layers of mudstone, are pale red (5R 6/2) with some pale reddish-brown (10R 5/4). Capped by light greenish-gray siltstone. 2300 lbs. (50 percent of −20 mesh concentrate not sorted); seed; *Spirorbis*; *O. platypternus*; xenacanth denticles and calcified cartilage; *Gnathorhiza* (more than one species?); *Eryops*?; *Diplocaulus*; microsaur; *Captorhinus*; *Dimetrodon*; 38 small indeterminate tetrapod jaws; coprolites.
SMU 81	Pale green (5G 7/2) to light greenish-gray (5G 8/1), slightly calcareous mudstone dominated by clay clasts and small (1 mm) flakes and vugs of gypsum? ("clay-pebble conglomerate"). Clasts are same color as mudstone. Layers of conglomerate alternate with red mudstone. Capped by light greenish-gray siltstone. 1200 lbs.; *Spirorbis*; *O. platypternus*; xenacanth spine fragments and denticles; *Gnathorhiza*; palaeoniscoid teeth and fish scale; *Diplocaulus*; *Dimetrodon*; coprolites.
SMU 82	*Dimetrodon*?
SMU 83	Pelycosaur.
SMU 84	Large indeterminate jaw fragment.
SMU 85	Indeterminate skull and jaw fragments.
SMU 86	*Lysorophus*.
SMU 87	*Diplocaulus*; captorhinid?
SMU 88	Pelycosaur.

UPPER VALE FORMATION

East end of Ignorant Ridge

SMU 89	Large captorhinomorph partial skull.

Ignorant Ridge area east of Mustang Creek

SMU 90	*Gnathorhiza*; *Diplocaulus*; indeterminate bones in carbonate/hematite matrix.
SMU 91	*Diplocaulus*; pelycosaur.
SMU 92	*O. platypternus*; *Dimetrodon*.
SMU 93	*O. platypternus*; *Diplocaulus*.
SMU 94	*O. platypternus*; amphibian scutes; coprolites.

3 miles north of Vera

SMU 95	*Diplocaulus*, *Lysorophus*
SMU 96	skeleton of a large captorhinomorph
SMU 97	*O. platypternus*

LOWER CHOZA FORMATION

North and south rim of Ignorant Ridge

SMU 98	*Diplocaulus*
SMU 99	Xenacanth calcified cartilage; 300 lbs. of sandstone/siltstone blocks: *Gnathorhiza*; indeterminate amphibian clavicles and pelycosaur jaws appear on surfaces of blocks.
SMU 100	Pale reddish-brown (10R 5/4) to dark reddish-brown (10R 3/4), with some pale red (5R 6/2) and minor light bluish-gray (5B 7/1), calcareous mudstone

dominated by small clay? pebbles ("clay-pebble conglomerate"). Overlain by greenish-gray (5G 8/1-6/1) siltstone; overlies reddish-brown (10R 5/4-3/4), noncalcareous, slightly silty mudstone with conchoidal fractures. 1200 lbs.; *O. platypternus*; palaeoniscoid scale; *Gnathorhiza*; *Diplocaulus*; amphibian scutes; isolated reptile teeth; coprolites.

West of Mustang Creek

SMU 101 *Diplocaulus.*
SMU 102 *Dimetrodon.*
SMU 103 Small amphibian? skull fragments; small coprolites.

2 miles north of Vera

SMU 104 *O. platypternus*; xenacanth calcified cartilage; amphibian jaw.

North side of North Wichita River

SMU 105 *Diplocaulus*; *Labidosaurus.*

A PREDATORY TERRESTRIAL FLATWORM, *BIPALIUM KEWENSE*, IN TEXAS: FERAL POPULATIONS AND LABORATORY OBSERVATIONS

Raymond W. Neck
Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744

Abstract.—Laboratory observations on behavior and records of feral populations of the terrestrial flatworm, *Bipalium kewense* Moseley, 1878, in Texas are reported. *Key words*: *Bipalium kewense*; terrestrial flatworm; predatory behavior.

While most biologists are aware of the existence of aquatic free-living flatworms (planarians), relatively few are familiar with terrestrial flatworms. The suborder Terricola (class Turbellaria, order Tricladida) comprises several hundred species (von Graff, 1899), several of which have become rather widespread as a result inadvertant dispersal with human commerce (Hyman, 1940, 1943, 1951, 1954).

The most common of these introduced flatworms in undoubtedly *Bipalium kewense* Moseley, 1878, of the family Bipaliidae. Moseley (1878) described this species from a moribund greenhouse specimen collected at the Royal Botanic Gardens at Kew, England. Subsequently, *B. kewense* has become so widespread that it has been described as the cosmopolitan land planarian (Hyman, 1951; Winsor, 1983a). Long assumed to be a native of some part of the Oriental region (Hyman, 1940), Winsor (1983a) restricted the native range of *B. kewense* from northern Vietnam to Kampuchea and possibly south through Malaysia.

B. kewense exhibits a honey brown background color with several dark brown to purplish brown longitudinal stripes (three narrow lines and two broad, diffuse bands). The anterior end is a characteristic semicircular shape and possesses a more uniform dark brown coloration. One of the larger specimens seen personally (from Austin) was 18 centimeters in length when moving but easily stretched to 30 centimeters when hanging down from the top of the terranium; width of body portion was approximately four millimeters. Hyman (1951) reported that *B. kewense* may reach a length of 35 centimeters.

A summary of literature reports of *B. kewense* for the United States reveals localities over most of the area east of the Mississippi River, except for some of the northernmost states; populations also are known from California (Winsor, 1983a). Records from the northern and western edge of its range in the United States are generally from greenhouses rather than outdoor sites. Such a restriction indicates a susceptibility to cold and dry conditions (to be expected in a species from the warm, moist regions of southeastern Asia). The published records from Texas

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are from "greenhouses" in Houston, which were the source of experimental animals (Campbell, 1965; Trammel and Campbell, 1971), although specimens have been purchased from a biological supply house in Houston (Phillips and Dresden, 1973). No published records of feral populations of *B. kewense* in Texas are known to me, although the presence of this species is well known to invertebrate zoologists in the state.

Relatively little information is available concerning the bionomics of *B. kewense.* Reproduction is normally asexual by fragmentation in subtropical and temperate areas (Hyman, 1940), although Connella and Stern (1969) observed cocoon formation and emergence of young. The taxa observed in this last study could have been *Bipalium adventitium*, which was described from introduced material in California (Hyman, 1943). *B. adventitium* has since established numerous populations in the northeastern United State (Klots, 1960). Laboratory populations of *B. kewense* have been utilized in various physiological investigations (Campbell, 1965; Trammell and Campbell, 1971; Phillips and Dresden, 1973). Kawaguti (1932) reported that *B. kewense* could survive water loss up to 45 percent of body weight.

The purpose of this communication is to present observations on predatory behavior and collection records of *B. kewense* in Texas.

Laboratory Observations

B. kewense feeds primarily (if not exclusively) on earthworms, on which it utilizes a collaginase to destroy the cuticle (Phillips and Dresden, 1973). It is known to be a minor pest on earthworm farms in the southern United States (Winsor, 1983a). Klots (1960) reported that *B. adventitium* fed on "small annelids,. . . slugs, insect larvae and the like." However, personal observations of *B. kewense* crawling over living slugs, *Sarasinula plebeius*, revealed no reaction from the flatworm.

Detailed observations on the predatory behavior of *B. kewense* have not been published. Wallen (1954) merely reported that "a full grown specimen could devour half of a five-inch earthworm within 30 minutes leaving a foamy mass." No attack description was provided although Wallen (1954) reported that *B. kewense* "usually moved from the anterior to the posterior end of the earthworm."

Laboratory observations revealed an interesting attack method. First contact occurred when an earthworm touched the body of a *B. kewense.* Although the earthworm initially appeared to be stuck to the flatworm, it later withdrew and continued onward with no apparent increased rate of locomotion. At the same time, however, the *B. kewense* began to move its anterior end toward the earthworm until its head came into contact with the worm. Then, *B. kewense* wrapped its body rapidly around the earthworm, which attempted eascape by increased rate of locomotion. *B.*

kewense wrapped itself around the prey, flattening out its body in an attempt to envelop the body of the earthworm. The *B. kewense* eventually was able to get all of its body criss-crossed to an extent that the earthworm was completely encased. Volume covered by the flatworm decreased as the earthworm was apprently consumed. Approximately 55 minutes following the attack, the *B. kewense* was again crawling around, whereas the earthworm was reduced to a layer of bubbles.

Predatory behavior of the related *Bipalium adventitium* was reported by Dindal (1970). Random contact followed by initial attack was similar to that observed for *B. kewense*, but *B. adventitium* did not appear to constrict earthworms. Average time of consumption was about 45 minutes.

Greatest mortality factor in feral populations of *B. kewense* is likely to be dessication. However, predation may have been sufficiently significant in its native habitat to evolve distastefulness. Winsor (1983b) reported vomiting in response to ingestion of *B. kewense* by a domestic cat. Personal observations revealed that both a Texas slider (*Chrysemys concinna texana*) and a tiger salamander (*Ambystoma tigrinum tigrinum*) refused to eat *B. kewense*. After snapping at *B. kewense*, the tiger salamander moved its head from side to side in an apparent rejection response.

TEXAS FERAL POPULATIONS

Cameron County.—*B. kewense* is known from two residential yards (separated by three kilometers) in Brownsville. Populations are much less dense than those found in Austin. Distribution is also much more spotty in the Brownsville area. Despite many earlier field surveys, *B. kewense* was not found in the Brownsville area until 24 December 1976; a subsequent population was found on 22 December 1977.

Comal County.—*B. kewense* was abundant under old railroad crossties in an open, disturbed area of level ground above Comal Springs, Landa Park, New Braunfels, on 12 June 1976.

Travis County.—*B. kewense* has a general distribution in the city of Austin. Whereas denser populations are characteristic of residential yards, flatworms also have been found in rock rip-rap areas on slopes below a city street (where no supplemental water is provided) and on a wooded slope along the shoreline of Town Lake. I have observed Austin populations since 1968.

Kendall County.—Several large specimens of *B. kewense* were found underneath logs lying on the second terrace of the Guadalupe River within Guadalupe River State Park on 24 April 1975. The significance of this record is its occurrence in a totally nonurban habitat. Origin of this population was likely from flood-borne specimens from an upstream urban area. Probabilities of persistence of this and similar populations are likely to be low, although population maintenance in protected mesic canyons is possible.

San Saba County.—Several small *B. kewense* were collected under doomed limbs at the edge of a pool of Gorman Creek, approximately 65 meters upstream of the falls in Gorman Falls State Park on 18 July 1985. This population probably originated with soil attached to exotic plants, for example, *Canna* sp. and *Colocasia* sp., which are well established at the site. Few population sources, if any, exist upstream on Gorman Creek; downstream dispersal along the Colorado River is unlikely because of the existence of a sheer 20-meter cliff at Gorman Falls.

Walker County.—A population of *B. kewense* was discovered in a woodland in a residential area of Huntsville near the junction of U.S. 190 and Texas 90 on 14 December 1977.

SUMMARY

Populations of *B. kewense* can be expected in residential areas of cities in the eastern two-thirds of Texas. The northern and western boundaries will be determined by degree of winter cold and periodic xeric conditions, respectively. It is of note that the only Oklahoma record is from a greenhouse (Wallen, 1954) and no records are known from New Mexico (Winsor, 1983a). Rarity of rural populations of *B. kewense* in Louisiana has been reported (Dundee and Dundee, 1963).

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VALIDATION OF DAILY RING DEPOSITION IN OTOLITHS OF WILD YOUNG-OF-THE-YEAR LARGEMOUTH BASS

J. Jeffery Isely and Richard L. Noble
Department of Wildlife and Fisheries Sciences, Texas A&M University,
College Station, Texas 77843

Abstract.—The formation of daily rings in otoliths of young-of-the-year largemouth bass (*Micropterus salmoides*) was observed in fish collected from three Texas ponds. Daily ring deposition began at hatching. Rings were deposited daily over a 152-day period in one pond and over 47- and 52-day periods in two other ponds. The 95 percent confidence interval for estimating the ring count from age for an individual fish was less than seven (plus or minus) rings. Distinguishable rings were deposited with daily regularity as long as growth was observed. Errors in ageing likely resulted from an inability to distinguish sub-daily from daily rings or from loss of resolution of rings that were compressed due to slow growth. *Key words*: otoliths; daily ring deposition; largemouth bass.

Until recently, ageing of fish has been restricted to the use of annular marks in bony (calcified) structures. Pannella (1971, 1974) suggested that, in addition to annual rings, the otoliths of some fish also contain daily rings, and that these daily rings were a universal property of teleost otoliths. Schmidt and Fabrizio (1980) reported a positive correlation between otolith ring count and time in samples from wild populations of largemouth bass (*Micropterus salmoides*) up to 80 days of age in New York. Miller and Storck (1982) verified daily ring deposition up to 100 days from otoliths of laboratory-raised largemouth bass held at ambient temperatures in Illinois. They found that ring formation began at hatching; however, the total complement of rings formed during the prolarval stage was visible for only 10 to 15 days after swim-up. Ages determined from otoliths tended to underestimate true age of older fish because of increased opacity of the otolith, which obscured some rings, and poor resolution of closely-spaced rings caused by slow growth at low temperatures.

Although daily growth rings appear to be deposited throughout the growing season and have been used to verify annulus formation in largemouth bass (Taubert and Tranquilli, 1982), previous efforts to verify the daily periodicity of ring deposition primarily have involved laboratory-raised fish. The purpose of this study was to investigate the formation of daily growth rings in otoliths of largemouth bass raised under field conditions rather than under the influence of cyclical laboratory activity.

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MATERIALS AND METHODS

To determine the age at first otolith ring deposition, otoliths were examined from largemouth bass larvae with a known hatching date. Largemouth bass embryos were collected on 19 April 1984 from a nest in a 0.5-hectare pond on the Southwest Texas State University campus. The embryos were incubated in two four-liter glass jars at ambient light and temperature. Upon hatching, fry were removed at approximatley two-day intervals for 11 days and stored in 70 percent ethanol for later analysis. Otoliths (sagittae) were later excised, placed in a small drop of immersion oil, and observed under a microscope (400×) with transmitted light.

Daily deposition of rings after 10 days was investigated by comparing the increments in mean ring counts with the time in days between samples collected from three 0.1-hectare ponds in central Texas. Pond K-2 was stocked with one male and two female mature largemouth bass in April of 1983 to produce a spawn. Brood fish were removed after fry were observed. Up to 30 fish were collected at about 25-day intervals from 26 May through 25 October 1983. Ponds SC-4 and SC-5 also were stocked in April 1983 with one male and four mature female largemouth bass to insure a spawn. As in pond K-2, brood fish were removed when fry were observed and up to 30 fry were collected at about 25-day intervals from 1 July through 22 August 1983.

Fish were collected by seining and were returned to the laboratory for processing. Otoliths were removed, stored in plastic vials until dry, then mounted on glass microscope slides with a small drop of thermoplastic cement. The otoliths were then prepared according to the methods of Taubert and Coble (1977) with modifications as described by Miller and Storck (1982), except that no. 600 carborundum paper was substituted for no. 600 grinding powder on a glass plate, and sections were not polished with a felt wheel. Rings were observed through a small amount of immersion oil. Otoliths that were unreadable due to thickness and opacity were repositioned so that the ground surface was attached to the slide, and the opposite surface was ground until a thin, readable section was produced. Ring counts were made in the posterior and ventral fields of the otolith; rings in the anterior field were poorly defined. The number of growth rings in each otolith was counted five consecutive times by the senior author and the median was determined. Because several factors negatively bias ring counts whereas few factors positively bias counts, the median was considered to produce a more accurate age estimate than the mean.

RESULTS AND DISCUSSION

Largemouth bass embryos began to hatch within 24 hours after collection and all had either hatched or died within 48 hours. Observations confirmed the report by Miller and Storck (1982) that otolith ring deposition begins at hatching. Ring deposition continued with daily regularity through the first 10 days of life (Table 1).

Seven samples of largemouth bass were collected from pond K-2 during a 152-day period (Table 2). The difference in the mean number of otolith rings between consecutive sampling dates corresponded closely to the time interval in days. The difference in mean otolith ring counts between consecutive samples and the time in days between samples was ≤ 6 in all cases. The deviation from expected count between the first and last sample, which represents a cumulative error, was -5 (Table 2). Although rings formed prior to swim-up were less distinct than other rings, no loss of resolution of nuclear rings in older fish (as seen by

TABLE 1. Number of rings visible in otoliths of largemouth bass three to 10 days old.

	Number of rings		
Age (days)	N	Mean	Range
3	1	3.0	-
5	3	6.0	-
7	3	8.3	8-9
10	4	11.3	11-12

Miller and Storck, 1982) was observed in this study and these rings were counted. The calculated ages, therefore, are age from hatching, not age from swim-up, as reported for largemouth bass by Miller and Storck (1982). Poor resolution of rings near the margin of the otolith often accounted for much of the variability in ring count. As these rings became imbedded in the otolith, resolution increased. Errors in ageing between consecutive samples, therefore, tended to be compensatory. Variability within the first four samples was low as indicated by the range and standard error (Table 2). Variability increased in the 29 August sample and remained high throughout the remainder of the study. Otolith rings deposited during August were compressed and difficult to distinguish, even at levels of magnification higher than normally used in this study (1000 ×). Poor resolution of these compressed rings may have caused an increase in the variance and an underestimation of the age of fish collected after 29 July.

The narrowing of growth rings was likely a result of a decline in growth during this period due to high water temperature and the density of fish in the pond. In order to reduce density, 500 fish were removed from pond K-2 on 30 September . Following the removal of these fish, growth of fish in the pond increased and well-defined daily rings were deposited thereafter. Variability continued to remain high because the region contributing the variation in ring count already had been imbedded in the otolith. Otolith rings again became compressed near the margin in the 25 October sample, indicating that first-year growth was nearly complete by that time.

Relationship between otolith ring spacing and growth may be useful in back-calculation of growth regimes. Miller and Storck (1982) found that total length of largemouth bass could be predicted from otolith radius. A relationship between the width of adjacent daily increments on otoliths and fish growth also has been observed for other species (Strusaker and Uchiyama, 1976; Taubert and Coble, 1977). Marshall and Parker (1982) found a high correlation between otolith diameter and fork length in sockeye salmon (*Oncorhynchus nerka*), and suggested that otolith ring spacing might be used to reconstruct detailed growth histories of individual fish.

TABLE 2. Number of rings observed in otoliths of young-of-the-year largemouth bass and the associated deviations from expected counts.

		Number of rings					Change		
Pond	Date	N	Mean	Range	SE	Change in count	in age (days)	Error	Sum of error
K-2	May 26	30	38.8	35-49	2.16				
	June 21	27	65.9	61-68	1.73	27	26	1	1
	July 6	15	81.7	80-83	0.80	16	15	1	2
	July 29	19	104.2	100-105	1.34	22	23	−1	1
	Aug. 29	25	132.1	122-137	4.38	28	31	−3	−2
	Sept. 27	25	164.0	153-170	3.78	32	29	3	1
	Oct. 25	10	186.2	176-195	4.96	22	28	−6	−5
SC-4	July 1	25	84.7	81-87	1.60				
	July 25	24	109.5	98-114	3.97	25	24	1	1
	Aug. 22	23	139.1	131-142	2.70	29	28	1	2
SC-5	July 1	33	63.3	55-74	3.83				
	July 25	25	83.5	77-88	2.83	21	24	−3	−3
	Aug. 17	26	106.0	98-109	2.82	22	23	−1	−4

Young largemouth bass were collected on three occasions from ponds SC-4 and SC-5 during a 52-day period (Table 2). The differences between mean otolith ring count and the time interval in days between consecutive samples was ≤ 1 from SC-4 and ≤ 3 from SC-5. The deviation from the expected difference between the first and last sample was two days in SC-4, and −4 days in SC-5. Resolution of growth rings was poor throughout the sampling period and variability was high in all samples.

Linear regression used to describe the relationship between the number of rings counted and time in days for data from all three ponds combined had a slope of 0.995 ($R^2 = 0.991$). The regressions used to describe the number of rings at a given time in days for each pond had slopes of 0.99, 1.05, and 0.90 for ponds K-2, SC-4, and SC-5, respectively. The 95 percent confidence interval for estimating the ring count from age for an individual fish was less than ±7 rings for the combined data and less than ±6 rings for the regression from an individual pond.

Whereas the slopes of the individual regressions were different from each other, and the slopes from ponds SC-4 and SC-5 were different from 1.0 ($\alpha < 0.05$), the power to detect a deviation in slope of 0.025 was >0.98. Although Schmidt and Fabrizio (1980) did not detect a significant deviation from daily deposition of rings, their power to detect a larger difference of 10 percent in the mean age of wild largemouth bass (estimated from their published statistics) was only 0.72. The deviation from a slope of 1.0 observed in this study was due to the power of the test and may not be biologically significant. Variation from the expected ring count of one per day likely resulted from a consistent inability to distinguish sub-daily from daily rings, or loss of resolution of rings that were closely spaced due to slow growth of fish in some samples, rather than from nondaily ring deposition.

CONCLUSIONS

Otolith rings appear to be deposited with daily regularity as long as the fish are growing. When growth slows, otolith increments become compressed and difficult to distinguish. Our results indicate that rings were generally deposited with daily regularity on otoliths in largemouth bass for up to 190 days, at which point rings became too closely spaced to accurately count due to slow growth of the fish. Cessation of growth also was used to explain why Miller and Storck (1982) could only verify the age of largemouth bass to 100 days, whereas Taubert and Tranquilli (1982) were able to do so for the length of the growing season (180 days). The use of daily growth rings to age fish becomes invalid when otolith rings become too compressed to be distinguished reliably, and this apparently occurs at different times for different populations.

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Present address of authors: Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695.

NOTES ON DISTRIBUTION AND NATURAL HISTORY OF SOME BATS ON THE EDWARDS PLATEAU AND IN ADJACENT AREAS OF TEXAS

Richard W. Manning, J. Knox Jones, Jr., Robert R. Hollander,
and Clyde Jones
The Museum and Departments of Biological Sciences and Museum Science, Texas Tech University, Lubbock, Texas, 79409

Abstract—Distributional and ecological observations are recorded for 10 species of bats from the Edwards Plateau and adjacent areas of south-central Texas. *Key words*: Chiroptera; distribution; natural history; Texas.

Except for studies of maternity colonies in large caves, little has been published concerning bats on the Edwards Plateau of south-central Texas since Blair's (1952) preliminary survey. For the past two years, most importantly in the summer of 1986, we have collected mammals on the Edwards Plateau and in immediately adjacent areas in order to gain a better understanding of distributional patterns in this interesting ecological region.

Among the materials thus far accumulated through our field efforts are specimens of 10 species of bats, a number of which represent noteworthy distributional records. These are reported here, along with additional specimens housed in The Museum of Texas Tech University that were collected earlier by other investigators. Pertinent comments on distribution and natural history are recorded. Unless noted otherwise, all dates in text relate to the year 1986.

We are grateful to the Graduate School of Texas Tech University for providing a summer research assistantship to Manning in support of this project. We also thank the office of the Vice President for Academic Affairs and Research at Texas Tech, the National Institutes of Health, and the Theodore Roosevelt Memorial Fund of the American Museum of Natural History (to Hollander) for financial support of field work.

Myotis velifer incautus (J. A. Allen, 1896)

The cave myotis is abundant and widely distributed on the Edwards Plateau (Blair, 1952), where breeding colonies of up to several thousand bats commonly are found. This species is a year-round resident of the region. We took lactating females as early as 19 May; a pregnant female netted on 28 May carried a single fetus (30 mm in crown-rump length). Both volant young and lactating females were captured on 19 and 21 June in Kimble County as they foraged for insects beneath a canopy of

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pecan trees. We observed these bats using cliff swallow nests as day roosts in August in Kinney County, a behavior previously reported by Pitts and Scharninghausen (1986).

Specimens examined, including bats from several new localities of record, are as follows: Crockett Co.: 19 mi. S, 16 mi. W Ozona, 1. Kimble Co.: Texas Tech Univ. Center at Junction, 35; 1 mi. S, 0.3 mi. W Junction, 2; 2.2 mi. S, 0.8 mi. E Junction, 13; 5 mi. S Texas Tech Univ. Center at Junction, 24; 8 mi. S Texas Tech Univ. Center at Junction, 8; Flemming Cave, 9.5 mi. S, 7 mi. W Junction, 3. Kinney Co.: 19 mi. SE Del Rio, 4. Llano Co.: Enchanted Rock, 1. Mason Co.: James River Bat Cave, 11 mi. S, 6 mi. W Mason, 10. Real Co.: Leakey, 19. Sterling Co.: 3.5 mi S, 4 mi. E Sterling City, 2. Sutton Co.: 3 mi. NE Sonora, 1. Val Verde Co.: 44 mi. N, 6 mi. W Del Rio, 1; Fawcett Cave, 36 mi. N Del Rio, 10; Dolan Springs, 36 mi. N, 6 mi. W Del Rio, 2; Comstrock R. R. Tunnel, 12 mi. W, 3 mi. S Comstock, 20; Fisher's Fissure, 2 mi. W Langtry, 9; 0.5 mi. E Langtry, 1; Mile [Eagle Nest] Canyon, 0.75 mi. E Langtry, 3; Comstock, 2.

Myotis yumanensis yumanensis (H. Allen, 1864)

The Yuma myotis is known from the Trans-Pecos region of Texas from Brewster, El Paso, Jeff Davis, Presidio, and Val Verde counties (Schmidly, 1977). This species occurs also on the southwestern edge of the Edwards Plateau to the east of the Pecos River. We captured three females, all lactating, in Val Verde County on 30 May.

Specimens examined, all from Val Verde County, are as follows: 0.5 mi. E Langtry, 3; Mile [Eagle Nest] Canyon, 0.75 mi. E Langtry, 1; R. R. Tunnel, 1.2 mi. W, 2.7 mi. N mouth of Pecos River, 2; junction of Rio Grande and Pecos rivers, 3; Comstock R. R. Tunnel, 12 mi. W, 3 mi. S Comstock, 21.

Lasionycteris noctivagans (Le Conte, 1831)

When this manuscript was in galley proof, Robert J. Baker and a group of students netted four silver-haired bats, all males, under a canopy of pecan trees in the floodplain of the South Llano River at the Texas Tech University Center at Junction, Kimble County. All were taken on the night of 17 May 1987. Presumably late northward migrants, these specimens provide the second locality of record for *L. noctivagans* from the Edwards Plateau, the other being an individual obtained on 20 March 1948 along the Medina River, about 18 mi. W Medina, Bandera County (Blair, 1952).

Pipistrellus hesperus maximus Hatfield, 1936

Western pipistrelles are widely distributed in Trans-Pecos Texas, having been recorded from all counties except Reeves and Pecos (Schmidly, 1977). Davis (1974) reported specimens from Val Verde, Uvalde, and Edwards counties on the southern edge of the Edwards Plateau. While netting in a steep-walled canyon, 0.5 mi. E Langtry, Val Verde County, we captured a lactating female on 30 May. Other bats taken at this location included *Myotis velifer*, *Tadarida brasiliensis*, and *Myotis yumanensis*. We also netted a lactating female on 5 July 1985 at a place 3 mi. S and 5 mi. E McCamey, Upton County. This locality lies to the east of Reeves and Pecos counties and helps to delineate the distribution of this species in the state.

Pipistrellus subflavus subflavus (F. Cuvier, 1832)

Blair (1952) reported this subspecies from only four counties on the Edwards Plateau—Bandera, Edwards, Kendall, and Kerr. Specimens available to us that help to clarify the distribution of this pipistrelle are as follows: Edwards Co.: Devil's Sinkhole, 3. Kimble Co.: Texas Tech Univ. Center at Junction, 6; 5 mi. S Texas Tech Univ. Center at Junction, 1. Real Co.: Leakey, 6.

At Junction, pipistrelles were netted under a canopy of large deciduous trees in the floodplain of the South Llano River. Those from Leakey were taken as described in the account of *Nycticeius*. The specimens listed above average somewhat paler, taking age and season into consideration, than do typical individuals of *P. s. subflavus* (see account below).

Pipistrellus subflavus clarus Baker, 1954.

According to Hall (1981), this race of the eastern pipistrelle has been recorded from Comstock, Devil's River, and Del Rio, all in Val Verde County and all east of the Pecos River, and 12 mi. W Comstock near the mouth of the Pecos. At hand are three specimens from Trans-Pecos, Texas, all males, that were taken in Fisher's Fissure, 2 mi. W Langtry, Val Verde County, on 12 April 1968.

The original description of this subspecies (Baker, 1954) was based on specimens from Coahuila, México, and immediately adjacent southern Texas. Compared with *P. s. subflavus*, it was noted to be of approximately the same size, but paler in color and with zygomata slightly more expanded laterally. Our three bats, all adults, are paler dorsally than spring-taken specimens from the Texas Panhandle but differ less from specimens from the Edwards Plateau to the east, suggesting the distinct possibility of an east-west cline in color across central Texas. We note little difference in the breadth of the zygomata in Texas material we have examined. Although we have not studied Mexican specimens of *clarus*, recognition of this race, based on information now available, should be carefully scrutinized.

Lasiurus borealis borealis (Müller, 1776)

Red bats are common in eastern Texas and are thought to be permanent residents of that area (Schmidly, 1983). Blair (1952) considered this species to be fairly common on the eastern part of the Edwards Plateau but reported specimens only from Kerr and Val Verde counties. We collected a lactating female on 11 June in Sterling County as it flew under a canopy of pecan trees. We also netted a series of 15 red bats in Real County (see account of *Nycticeius*) in July and August. This sample included adult males and females plus young-of-the-year of both sexes. A female taken in Kimble County on 21 May carried four embryos (crown-rump length 20 mm).

Specimens examined are as follows: Kimble Co.: Texas Tech Univ. Center at Junction, 14; 5 mi. S Texas Tech Univ. Center at Junction, 7; 17 mi. SE Junction, 2. Real Co.: Leakey, 15. Sterling Co.: 4 mi. S, 4 mi. E Sterling City, 1. Sutton Co.: Sonora, 1.

Lasiurus cinereus cinereus (Palisot de Beauvois, 1796)

Davis (1974) reported this species as a "relatively rare migrant through Texas." Schmidly (1977), however, reported the hoary bat as resident in the warm months in "wooded, montane areas" of the Trans-Pecos region. On 19 April, we netted a barren female over a small cattle pond, which was surrounded by mesquite and in desert scrub habitat, in Crockett County. A male taken on 19 September in Sutton County had numerous small cactus spines in its wing membranes and several imbedded in the abdominal fur. That same evening another hoary bat was observed to hit the mist net we had stretched over a concrete tank, fall into the water, and take to the air from the surface, a behavior previously reported by Schmidly (1983).

The only information on reproduction in the state by this species outside the Chisos and Guadalupe mountains of far western Texas (pregnant females captured in April and June, respectively—Schmidly, 1977) is of a gravid female obtained on 19 April 1978 in Big Thicket National Preserve (Schmidly, 1983). It is noteworthy, therefore, that two females taken on 20 and 21 May in Kimble County were pregnant, carrying two fetuses each that measured 9 and 10 mm, respectively, in crown-rump length. While these and other females mentioned above may have been migrants, the presence of pregnant individuals in Texas as late as May and June strongly underscores the possibility that young are born in the state.

Specimens examined are as follows: Crockett Co.: 5 mi. S, 5 mi. E McCamey, 1. Kimble Co.: Texas Tech Univ. Center at Junction, 3; 5 mi. S Texas Tech Univ. Center at Junction, 1. Sutton Co.: 13 mi. W Sonora, 1.

Nycticeius humeralis humeralis Rafinesque, 1818

The evening bat is known to occur primarily to the east of the Balcones Escarpment in Texas (Schmidly, 1983). It has been reported only from Kerr and Bandera counties on the Edwards Plateau (Blair, 1952; Davis, 1974). We netted five evening bats under a cypress canopy along Leakey Creek at Leakey, Real County (see Fig. 1). One young female was taken there on 10 July, and a male and three females were captured on 20 August. An additional five evening bats (three females, two males) were netted over a tree-lined stretch of Pinto Creek, 19 mi. SE Del Rio, in Kinney County, on 22 August. The specimens here reported represent the westernmost records of this species in Texas.

Antrozous pallidus pallidus (Le Conte, 1856)

The pallid bat is known to occur eastward on the Edwards Plateau at least as far as Kerr and Kimble counties (Martin and Schmidly, 1982). It is widely distributed in the western part of the region. We took lactating females in Kimble County on 19 May, 19 June, and 21 June. A female taken there on 21 May carried two fetuses (29 mm in crown-rump length).

On the night of 30 June, while netting for bats underneath a bridge over the Pecos River in Crockett County, we noted that pallid bats were using the underside of the bridge as a night roost. After collecting several, we observed bat activity for one-half hour or so. Near the end of that time, approximately two hours after sunset, a large female (forearm 51 mm, weight 21 grams) *Antrozous* alighted under the bridge closely followed by two smaller individuals (forearms 48 mm, weights 14 and 12 grams), which immediately began to nurse from her. We collected these three bats. Examination of the stomachs of the young animals (both males) revealed that the lower portion was filled with insects but that the upper part contained a layer of milk.

This observation indicates that young *Antrozous* both forage for insects and continue to nurse for a time after they become volant. It also implies a strong mode of communication, even while on the wing, between members of a family group, which evidently forage together in mid-summer (see O'Shea and Vaughan, 1977).

Specimens examined from the Edwards Plateau and adjacent areas, in addition to those reported by Martin and Schmidly (1982), are as follows: Crockett Co.: 5 mi. N, 4 mi. W Iraan, 8. Kimble Co.: Texas Tech Univ. Center at Junction, 64; 1 mi. S Texas Tech Univ. Center at

FIGURE 1. Photograph of the place where bats were netted along Leakey Creek, Real County. *Myotis velifer*, *Pipistrellus subflavus*, *Lasiurus borealis*, *Nycticeius humeralis*, and *Tadarida brasiliensis* were collected at this site, which may be the southwesternmost locality of occurrence in Texas of bald cypress and Spanish moss.

Junction, 1; 5 mi. S Texas Tech Univ. Center at Junction, 7; 17 mi. SE Junction, 1. Upton Co.: 3 mi. S, 5 mi. E McCamey, 8.

Tadarida brasiliensis mexicana (Saussure, 1860)

The Brazilian free-tailed bat is the most common chiropteran on the Edwards Plateau. Blair (1952) stated that *T. brasiliensis* is a year-round resident of the region. We, however, doubt that this is true, especially in the western areas with which we are most familiar. Short et al. (1960) suggested that southward migration of this species from the plateau may follow a westerly path. A nonpregnant female and a male captured on 18 March in Upton County probably represent early migrants into (or through) that area. Lactating females were taken as late as 10 July (Real County).

Bracken Cave, Comal County, and Ney Cave, Medina County, each are known to house maternity colonies that have been estimated to contain 20 to 30 million free-tailed bats (Raun and Baker, 1959). Blair (1952), Short et al. (1960), and McCracken (1984) listed other caves on the Edwards Plateau that serve as maternity sites.

Specimens examined, many of which represent new localities of record, are as follows: Blanco Co.: Davis Cave, vic. 11 mi. N, 10 mi. W Johnson

City, 65. Comal Co.: Bracken Cave, vic. 2 mi. S, 11 mi. W New Braunfels, 70. Crockett Co.: 5 mi. S, 5 mi. E McCamey, 12. Kimble Co.: Texas Tech Univ. Center at Junction, 11; 1 mi. S, 0.3 mi. W Junction, 1; 5 mi. S Texas Tech Univ. Center at Junction, 6. Kinney Co.: 19 mi. SE Del Rio, 1. Mason Co.: James River Bat Cave, 11 mi. S, 6 mi. W Mason, 13. Medina Co.: Ney Cave, 61. Midland Co.: Midland, 1. Real Co.: Leakey, 1. Sterling Co.: 3.5 mi. S, 4 mi. E Sterling City, 22. Sutton Co.: 3 mi. NE Sonora, 25; 13 mi. W Sonora, 2; 3 mi. E Sonora, 1. Upton Co.: 3 mi. S, 5 mi. E McCamey, 2. Uvalde Co.: Frio Cave, 19. Val Verde Co.: 5 mi. S, 3 mi. E Pandale, 1; Pecos River, near Pandale, 2; 44 mi. N, 6 mi. W Del Rio, 2; Fern Cave, 40 mi. NW Del Rio, 1; Comstock R. R. Tunnel, 12 mi. W, 3 mi. S Comstock, 28; Fisher's Fissure, 2 mi. W Langtry, 2; 0.5 mi. E Langtry, 2; Mile [Eagle Nest] Canyon, 0.75 mi. E Langtry, 8.

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GENERAL NOTES

ADDITIONAL RECORDS OF TICK (ACARI: IXODIDAE, ARGASIDAE) INGESTION BY WHIPTAIL LIZARDS, GENUS *CNEMIDOPHORUS*

CHRIS T. MCALLISTER AND JAMES E. KEIRANS

Renal-Metabolic Laboratory (151-G), Veterans Administration Medical Center, 4500 S. Lancaster Road, Dallas, Texas 75216, and Department of Biological Sciences, North Texas State University, Denton, Texas 76203, and Department of Health and Human Services, Public Health Service, National Institutes of Health, National Institute of Allergy and Infectious Diseases, Department of Entomology, Museum Support Center, Smithsonian Institution, Washington, D.C. 20560

There are few reports of reptiles ingesting ticks. In Africa, Norval (1976) reported that the yellow-throated plated lizard, *Gerrhosaurus flavigularis*, would feed on the ixodid or hard tick species *Haemaphysalis muhsami, Amblyomma nuttalli*, and *A. hebraeum* and Norval and McCosker (1983) observed the rainbow skink, *Mabuya quinquetaeniata margaritifer*, feeding on the African cattle tick, *A. hebraeum*. In the United States, Degenhardt and Jones (1972) recorded "ticks" in the stomach contents of the dunes sagebrush lizard, *Sceloporus graciosus arenicolous*, and McAllister (1987) reported the first instance of the argasid or soft tick *Otobius megnini* being eaten by the Texas spotted whiptail lizard, *Cnemidophorus gularis gularis*. Herein we report two additional cases of predation on ticks by two species of whiptail lizards.

An adult male *C. g. gularis* (snout-vent length, 85 mm) was obtained by F. S. Hendricks on 19 May 1974, 20.8 kilometers east of Soledad at an elevation of 665 meters in the state of Coahuila, Mexico. The stomach contained a single female *Dermacentor parumapertus*. The presence of hair in the stomach of the lizard along with this tick suggests that the tick may have been taken from a dead host.

The other situation involved an adult female Colorado checkered whiptail, *C. tesselatus* (pattern class "C"; snout-vent length, 98 mm), taken by J. F. Scudday on 26 June 1974 at the Mansfield Ranch, 32.5 kilometers northwest of Vega, Oldham Co., Texas. Five (two male, two female, one nymph) spinose ear ticks, *Otobius megnini*, were found in the stomach. Fecal material from the rectum appeared also to contain digested tick remains, which may indicate feeding on ticks on more than one occasion. The finding of two males, two females, and one nymph of *O. megnini* in the stomach of this lizard suggests that it probably scavenged these ticks from the ground.

The senior author found no additional ticks in more than 300 whiptail lizards of six species. The frequency of ticks in the diet of *Cnemidophorus* sp. is estimated to be less than one percent. Further, the comprehensive dietary studies of Milstead (1957, 1965), Medica (1967), Milstead and Tinkle (1969), and Scudday and Dixon (1973) on various species of *Cnemidophorus* did not list ticks as a prey item of whiptail lizards. These lizards utilize the "widely-foraging" strategy of obtaining prey (MacArthur and Pianka, 1966) and have a seasonal variation in prey consumed, indicative of temporally abundant Arthropoda.

Reference specimens are deposited in the Smithsonian Institution Acarological Collections as follows: *O. megnini* (RML 118495); *D. parumapertus* (RML 118399). The lizards are deposited in the Texas Cooperative Wildlife Collection and the Sul Ross State University Collection as follows: *C. g. gularis* (TCWC 46905); *C. tesselatus* (SRSU 3392).

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A SPECIMEN OF WHITE-WINGED DOVE, *ZENAIDA ASIATICA*, FROM ARCHER COUNTY, TEXAS

FREDERICK B. STANGL, JR., AND WARREN PULICH

Department of Biology, Midwestern State University, Wichita Falls, Texas 76308,
and *Department of Biology, University of Dallas, Irving, Texas 75062*

The white-winged dove (*Zenaida asiatica*) occurs in Texas primarily in the Rio Grande Valley and South Texas Plains, and locally north to Bexar County, with scattered sightings from the southern Panhandle (Arnold, 1984). In Oklahoma, there are sight records from Greer and Jackson counties (Wood and Schnell, 1984).

A white-winged dove was shot by a hunter 1 mi. S Holliday, Archer Co., Texas, on 21 September 1986. Apparently, it was mistaken for a mourning dove (*Zenaida macroura*), but the left wing was saved, and was presented to the Midwestern State University Collection of Birds. The specimen (MWSU 1073) represents the only voucher record known to us of a white-singed dove from as far north in Texas as Archer County.

With the exception of a specimen collected from the Texas High Plains on 17 May 1890 in Armstrong County (Oberholser, 1974), all other extra-limital records are sight records. Oberholser's original manuscript (filed on microfilm at the University of Dallas, Irving, Texas) indicated that the J. K. Strecker collection at Baylor University, Waco, Texas, may have been the repository for the specimen in question. A check at Baylor and six other

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major museums with avian material from Texas did not uncover the alleged specimen. We believe the example from Armstrong County may no longer exist.

We thank curators at the following museums for their assistance: American Museum of Natural History, Cincinnati Museum of Natural History, Strecker Museum of Natural History, Texas A&M University, University of Texas, U.S. National Museum, and Yale University.

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ANOLIS SAGREI (SAURIA:IGUANIDAE) ESTABLISHED IN SOUTHERN TEXAS

Ken King, David Cavazos, and Frank W. Judd
Department of Biology and Coastal Studies Laboratory
Pan American University, Edinburg, Texas 78539

Anolis sagrei, the brown anole, is native to Cuba, Jamaica, and the Bahamas. The species has been introduced and established in Florida and in several localities from southern Mexico to Honduras (Conant, 1975). The brown anole was first reported in the United States by Garman (1887), who listed the locality as "Florida Keys." Godley et al. (1981) reviewed the distributional status of *A. sagrei* in Florida and reported that it now inhabits much of the peninsular part of that state as disjunct colonies that generally are confined to urban settings. Wilson and Porras (1983) stated that *A. sagrei* is now the most common reptile in urban areas of southeastern Florida. Surprisingly, there were no records of the brown anole in other Gulf Coast states until Dixon (1987) reported the species in Houston, Texas, in 1985. His specimens were found in a plant nursery by J. W. Werler. At the urging of Dr. Dixon we initiated a survey of plant nurseries in southern Texas to ascertain if *A. sagrei* was present. Plant nurseries were deemed likely places for residency of the brown anole because Godley et al. (1981) suggested that one of the primary means of dispersal was through the transport of lizards or their eggs in ornamental plants via the commercial nursery trade. During the fall of 1986, we searched nurseries in Brownsville and Harlingen (Cameron County), Edinburg, McAllen, and Mission (Hidalgo County) and San Antonio (Bexar County) Texas, for *A. sagrei*.

We found brown anoles at one nursery in each of three cities—Brownsville, Harlingen, and San Antonio. We collected three males and two juveniles from the Harlingen nursery on 19 October 1986. Two of the males were sent to J. R. Dixon, Texas A&M University, who confirmed that the lizards were indeed *A. sagrei*, but he noted that they were not of the same genetic stock as specimens from Tampa, Florida. Both adults and juveniles were observed, captured, and released at the Brownsville nursery on 18 October 1986. Several juvenile *A. sagrei* were observed at the San Antonio nursery on 10 October 1986. Two were captured, but the owner denied our request to keep the specimens. On 1 November 1986, we collected 18 *A. sagrei* from the Harlingen nursery—nine adult males, six adult females,

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and three juveniles. The population at this nursery is large. Brown anoles were seen throughout the 2.4 hectares of grounds. We could easily have captured additional specimens. Furthermore, the owner and an employee reported that they had populations established at their homes.

There is no question that breeding populations of *A. sagrei* are now established in Cameron County, Texas, and it is likely that juveniles we saw in San Antonio reflect a breeding population there. The Brownsville and Harlingen localities are only about 48 kilometers apart and both are near ports on the coast. Conversely, the San Antonio locality is 386 kilometers north (inland) from Harlingen. Interviews with the owners and employees of the nurseries convinced us that brown anoles have been present at each nursery for about three years. In December 1983, southern Texas experienced a devastating freeze that killed most of the citrus trees and many other introduced tropical plants, including palms. *Anolis sagrei* may have been introduced to southern Texas when nurserymen replenished their stocks of ornamental tropical plants from Florida following the 1983 freeze. Alternatively, the lizards or their eggs may have been introduced via ships visiting the ports of Brownsville or Harlingen. Multiple introductions by both methods is a distinct possibility. Furthermore, *A. sagrei* may have become established at other localities in southern Texas and along the Texas Gulf Coast. Hopefully, this note will help stimulate interest in surveys for the brown anole so that its range in Texas can be ascertained and its spread or decline documented.

We thank James R. Dixon for confirming our identification of *Anolis sagrei*, suggesting this study, and reviewing an earlier draft of the manuscript.

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FIRST RECORD OF *CENTROPAGES TYPICUS* KROYER (COPEPODA: CENTROPAGIDAE) IN THE GULF OF MEXICO

David C. McAden, George N. Greene, and William B. Baker, Jr.
Houston Lighting & Power Company, Environmental Protection Department,
P.O. Box 1700, Houston, Texas 77001

On two dates in September, three dates in October, and three dates in November 1985, the calanoid copepod, *Centropages typicus* Kroyer, previously unknown from the Gulf of Mexico, was collected in plankton samples from the lower Colorado River of Texas, approximately 26.4 kilometers upstream of the mouth of the river and 25.9 kilometers downstream of the Port of Bay City in Matagorda County, Texas. A total of 91 specimens was collected.

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C. typicus is a cool-water species known to occur along the Atlantic coasts of the United States and Europe (Van Engle and Tan, 1965; Sars, 1902). Bowman (1971) stated that *C. typicus* does not normally occur south of Cape Hatteras, North Carolina. An extensive literature review and personal communications revealed no previous reports of *C. typicus* from the Gulf of Mexico. Two species of the genus *Centropages, C. hamatus* and *C. velificatus*, are known to occur in the neritic waters of Texas (R. D. Kalke, University of Texas Marine Science Institute, Port Aransas, personal communication). NUS Corporation (1976), in an earlier study conducted at the same location and additional locations upstream and downstream, reported no *C. typicus*, but did record *C. hamatus* and *C. velificatus*.

C. typicus was collected from the Colorado River in depths ranging from the surface to the bottom (approximately 20 feet). The range of water temperature over which it was found was 19.5 to 29.7°C. Salinity varied from 1.6 parts per thousand (surface) to 30.6 (bottom). Seventy-nine of the 91 specimens collected were taken in salinities above 19.0 parts per thousand. Sixty of the 91 were from a single bottom sample collected on 6 November 1985 (water temperature, 19.5°C; salinity, 21.6 parts per thousand). In samples collected on 31 October and 1 November 1985, which contained a total of 12 individuals of *C. typicus*, there were also nine specimens of *C. velificatus*. These were the only samples in which more than one species of *Centropages* occurred.

Exactly when *C. typicus* first appeared in the lower Colorado River and how it was introduced is not known. It may have been transported via ballast tanks on ships or barges from the Atlantic coast of the United States. Additional sampling is necessary to determine if *C. typicus* has established a resident population in the lower Colorado River.

Thirty specimens were deposited in the United States National Museum of Natural History (USNM no. 231086). The authors wish to acknowledge Dr. Abraham Fleminger of the Scripps Institution of Oceanography and Dr. Thomas Bowman of the Smithsonian Institution for confirming the identification of specimens sent to them. Dr. Frank G. Schlicht of Houston Lighting & Power Company contributed valuable editorial comments and Richard D. Kalke of the University of Texas Marine Science Institute at Port Aransas, Texas, shared with us his knowledge of the genus *Centropages* from the coastal waters of Texas.

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EVIDENCE OF COMMUNAL NESTING AND WINTER-KILL IN A POPULATION OF *BAIOMYS TAYLORI* FROM NORTH-CENTRAL TEXAS

Frederick B. Stangl, Jr., and Stephen Kasper
Department of Biology, Midwestern State University, Wichita Falls, Texas 76308

The pygmy mouse, *Baiomys taylori*, may become locally abundant under favorable conditions. Although captive individuals are known to be highly tolerant of each other, we are unaware of any records of communal nesting under natural conditions.

On 31 January 1987, a large (25 centimeters in diameter), globular surface nest of fine grasses was found under an inverted wooden crate on the Texas A&M University Agricultural Research Station, 10 mi. N Throckmorton, Throckmorton Co., Texas. The single hollow nest chamber contained seven dead adult pygmy mice, in similarly early stages of decomposition. All but two were partially eaten, but whether from cannabalism or from opportunistic scavenging by other small mammals was impossible to determine.

Just previous to our discovery, the research station experienced four days (15-18 January) of continued subfreezing temperatures and frozen precipitation (mostly in the form of freezing rain), forming ice sheets of up to one inch in thickness. The following interval was characterized by cool days and subfreezing nights. The mice apparently huddled together for warmth. The cause of death is not known; possibly the seven animals succumbed to hypothermia, or starved to death because of difficult foraging conditions or by becoming trapped under the ice-covered box.

Baiomys taylori is mostly subtropical in distribution, although the expansion of its range northward and westward in Texas (Austin and Kitchens, 1986; Cleveland, 1986; Dalquest and Horner, 1984; Hart, 1972; Hollander et al., 1987; Stangl et al., 1983) and into Oklahoma (Stangl and Dalquest, 1986) is well-documented. However, Stangl and Dalquest (1986) noted that inhospitable weather might periodically halt or reverse the progress of range expansion, giving the decline in numbers of specimens from north-central Texas in recent years as indirect evidence.

The lack of similar records elsewhere for communal nesting and cases of winter-kill in *Baiomys taylori* suggests to us that these occurrences are uncommon, and may be seasonally-induced, geographic phenomena along the northern margins of the range of the species. It would be premature to claim that our observation was more than an isolated incident. However, we note that previous trapping in the vicinity (November 1986) indicated high population densities of the pygmy mouse. Subsequent collecting efforts through April 1987 have failed to produce any additional specimens.

We gratefully acknowledge Drs. Rod Heitschmidt and Bill Pinchak for the invitation to collect specimens on the Texas A&M University Research Station. Walter W. Dalquest, Arthur G. Cleveland, and Dawn Morris critically reviewed the manuscript. Weather data was kindly provided by Dorothy Keeter, Throckmorton County weather recorder.

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NEW WESTERN DISTRIBUTIONAL RECORD OF *TERRAPENE CAROLINA TRIUNGUIS*

Michael R. Gannon
Department of Biological Sciences and The Museum, Texas Tech University,
Lubbock, Texas 79409

A specimen of the three-toed box turtle, *Terrapene carolina triunguis*, was obtained at the Texas Tech University Center at Junction, a mile south of Junction, Kimble Co., Texas (30° 30′N, 99°45′W). The individual, a male, was taken on 25 June 1986 from a trail transversing a wooded area approximately 100 meters north of the South Llano River. It was deposited in the herpetology collection of The Museum, Texas Tech University (TTU 11298).

Of the four subspecies of *T. carolina* that occur in the United States, *T. c. triunguis* ranges farthest west, reaching into parts of eastern Texas (Conant, 1975; Ernst and Barbour, 1972; Raun and Gehlbach, 1976). This specimen is the first record from Kimble County and marks a western range extension of nearly 100 miles. I thank M. R. Willig and M. J. van Staaden for reviewing this manuscript. I also thank J. R. Dixon for furnishing current distributional records.

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FIRST RECORDS OF THE FLAMMULATED OWL (*OTUS FLAMMEOLUS*) IN THE CENTRAL TRANS-PECOS OF TEXAS

Donna Burt, D. Brent Burt, Terry C. Maxwell, and Ross C. Dawkins
Departments of Biology and Chemistry (RCD), Angelo State University,
San Angelo, Texas 76909.

On 14 September 1986, an adult flammulated owl (*Otus flammeolus*) in red phase was captured in a mist net in upper Madera Canyon of the Davis Mountains, 26 km. NW Fort

Davis, Jeff Davis Co., Texas. This locality was at an elevation of 1920 meters in an association of ponderosa pine (*Pinus ponderosa*), pinyon pine (*P. cembroides*), and alligator juniper (*Juniperus deppeana*). The owl was captured under ponderosa pines within 100 meters of a stream bed, banded (U.S. Fish and Wildlife Service band no. 1433-13669), photographed, and released. This is the first record of a flammulated owl from the Davis Mountains.

On 19 April 1987, an adult female flammulated owl, also in red phase, was collected 16 km. SW Alpine, Brewster Co., Texas. This locality, 58 kilometers southeast of the Madera Canyon site, was at an elevation of 1675 meters. The owl was captured in a mist net placed between buildings of a church encampment in an oak (*Quercus* sp.) grove along Toronto Creek. The specimen is deposited in the collection of birds at Angelo State University (ASNHC 504). This is the first record for Brewster County outside of the Chisos Mountains, Big Bend National Park.

This migratory species has been reported as a regular but rare and local summer breeding resident (late March through September) at high elevations (above 1900 meters) in the Guadalupe and Chisos mountains (Wauer, 1973; Oberholser, 1974; Newman, 1979; Arnold, 1984), and as irregular in the Chinati Mountains (Oberholser, 1974). Although the dates of our records preclude speculation on the breeding status of the species in the central Trans-Pecos, they do suggest that the species occurs regularly there.

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———. 1975. An introduction to the study of plants. John Wiley and Sons, New York, xx+386 pp.

Jones, T. L., A. L. Bain, and E. C. Burns. 1976. Grasses of Texas. Pp. 205-265, *in* Native grasses of North America (R. R. Dunn, ed.), Univ. Texas Studies, 205:xx+1-630.

Smith, J. D. 1973. Geographic variation in the Seminole bat, *Lasiurus seminolus*. J. Mamm., 54:25-38.

Smith, J. D., and G. L. Davis. 1985. Bats of the Yucatan Peninsula. Occas. Papers Mus., Texas Tech Univ., 97:1-36.

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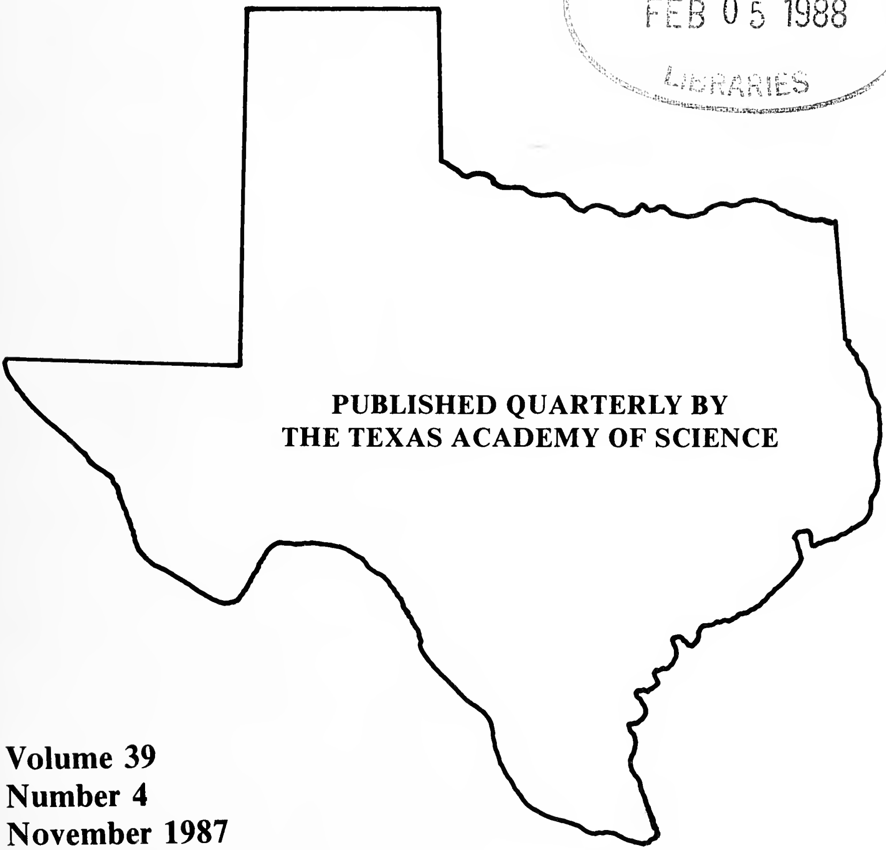

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LONG-PERIOD SURFACE-WAVE PHASE-VELOCITY PARTIAL DERIVATIVES WITH RESPECT TO EARTH PARAMETERS

Doo Jung Jin
c/o Commander, EUSA-TNT (J2), APO, San Francisco, California 96301-0092

Abstract.—Rodi et al. (1975) have developed a fast and accurate method for computing group-velocity partial derivatives with respect to earth parameters when corresponding phase-velocity partial derivatives are known. Novotný (1970) derived an analytical method for phase-velocity partials, but he limited his algorithm to Love waves, which are much simpler than Rayleigh waves. Employing the same approach as Novotný's, Jin and Herrin (1980) formulated a new exact method for the computation of Rayleigh-wave phase-velocity partial derivatives with respect to earth parameters. Since the publication of the last paper, many inquiries about the details of the method have been received. This paper attempts to provide a set of convenient formulae to be used in the method. *Key words*: partial derivatives; phase velocity; surface waves; dispersion.

In the inversion of surface-wave dispersion observations to determine the structure of the earth, it is necessary to compute the partial derivatives of phase and/or group velocity with respect to various earth parameters. Because a fast and accurate method has been developed for computing group-velocity partial derivatives when corresponding phase-velocity partial derivatives are known (Rodi et al., 1975), there was a demand for a simple new method for the computation of exact phase-velocity partial derivatives. I have formulated a new convenient analytical method for this purpose and applied it successfully to an inversion problem (Jin and Herrin, 1980). Although the algorithm was described in this cited reference, detailed formulae were not included due to limited space. Since the publication of the referred paper, many inquiries about the details of the method have been received. It seems beneficial to the scientific community to publish the details of the method. The present paper aims to satisfy this need.

In the earth model in which the earth consists of many elastic, homogeneous and isotropic parallel layers on a homogeneous and isotropic half-space, earth properties may be defined by longitudinal and transverse wave velocities, density, and thickness of the component layers. Various methods have been proposed in computing the phase-velocity partial derivatives with respect to the above model parameters.

Dorman and Ewing (1962), followed by Brune and Dorman (1963), calculated the changes in phase velocity due to perturbation of each physical parameter, while retaining the remaining parameters constant. This method is time-consuming. On the basis of Jeffrey's (1961)

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theoretical suggestion that Rayleigh's principle can be used to find expressions for the effects of small changes of the elastic properties on the phase velocity, Anderson (1964), Takeuchi et al. (1964), Harkrider (1968), and Anderson and Harkrider (1968) approached the problem by using the energy integral technique. McEvilly (1964) has used a combination of the above two methods. Bloch et al. (1969), Der et al. (1970), Der and Landisman (1972), and Knopoff (1972) computed phase-velocity partial derivatives but they have not described the algorithm they employed. Novotný (1970) derived exact expressions for phase-velocity partials in a different way by taking advantage of Thomson-Haskell matrices (Thomson, 1950; Haskell, 1953). But Novotný's paper limited itself to the derivation of partials for Love waves, which are much simpler than Rayleigh waves.

To provide convenience to the reader and to make this paper complete, the new method formulated for Rayleigh waves will first be presented, and then formulae needed in this method will be given. Employing double precision in computer coding, the use of the Haskell layer matrix method has not shown any numerical difficulties (Thrower, 1965; Dunkin, 1965; Gilbert and Backus, 1966; among others) on the commonly investigated long-period band of 10 to 100 seconds.

METHOD

Harkrider (1964) derived a matrix equation for the dispersion of Rayleigh waves, which may be expressed as follows:

$$F(c, \omega, \alpha_m, \beta_m, \rho_m, d_m) = NK + L^*M^* - T^*(G^*N - L^*H) \qquad (1)$$

where

$$c = c(\omega, \alpha_m, \beta_m, \rho_m, d_m),$$

$$T^* = c^2 \rho_0 \tan P_0 / r_{\alpha 0},$$

and

$$\begin{aligned} L &= \gamma_n r_{\alpha n} A_{11} + (\gamma_n - 1) A_{21} - (r_{\alpha n} A_{31} - A_{41})/(c^2 \rho_n), \\ K &= \gamma_n r_{\alpha n} A_{12} + (\gamma_n - 1) A_{22} - (r_{\alpha n} A_{32} - A_{42})/(c^2 \rho_n), \\ G &= \gamma_n r_{\alpha n} A_{13} + (\gamma_n - 1) A_{23} - (r_{\alpha n} A_{33} - A_{43})/(c^2 \rho_n), \\ N &= -(\gamma_n - 1) A_{11} + \gamma_n r_{\beta n} A_{21} + (A_{31} + r_{\beta n} A_{41})/(c^2 \rho_n), \\ M &= -(\gamma_n - 1) A_{12} + \gamma_n r_{\beta n} A_{22} + (A_{32} + r_{\beta n} A_{42})/(c^2 \rho_n), \\ H &= -(\gamma_n - 1) A_{13} + \gamma_n r_{\beta n} A_{23} + (A_{33} + r_{\beta n} A_{43})/(c^2 \rho_n). \end{aligned} \qquad (2)$$

Here ω is the angular frequency, c phase velocity, α and β velocities of compressional and shear waves, ρ density, d thickness of a layer;

$$\gamma_m = 2(\beta_m / c)^2,$$
$$P_m = k\, d_m\, r_{\alpha m},$$

where k represents the wave number:

$$r_{\alpha m} = \begin{cases} (c^2/\alpha_m^2 - 1)^{1/2} & c > \alpha_m \\ -\,i(1 - c^2/\alpha_m^2)^{1/2}, & c < \alpha_m, \end{cases}$$

$$r_{\beta m} = \begin{cases} (c^2/\beta_m^2 - 1)^{1/2} & c > \beta_m \\ -\,i(1 - c^2/\beta_m^2)^{1/2}, & c < \beta_m; \end{cases}$$

where $i = (-1)^{1/2}$:

$$A = a_{n-1}\, a_{n-2} \cdots a_1$$

with a_m designating the Haskell's layer matrix for the mth layer; and subscripts m, n and 0 refer to the mth solid layer, half-space and liquid surface layer, respectively. In order to minimize typographical requirements, a compound subscript, α_m, is used where a subscripted subscript is appropriate. An asterisk superscript is used to transform an imaginary quantity into a real one such that $Z^* = Z/i$ for an arbitrary imaginary quantity Z.

Because $T^* = 0$ for the earth model in which the liquid surface layer does not exist, considering (1) is sufficient for earth models both with and without ocean. From (1),

$$\frac{\partial c}{\partial x} = -\frac{\partial F}{\partial x} \Big/ \frac{\partial F}{\partial c}$$

where x designates one of the earth parameters, α, β, ρ and d.

If we define two product matrices A_m and B_m such that

$$A_m = a_m\, a_{m-1} \cdots a_1,$$
$$B_m = a_{n-1}\, a_{n-2} \cdots a_m,$$

then

$$A = B_{m+1} \cdot a_m \cdot A_{n-1},$$

$$\frac{\partial A_{ij}}{\partial x_m} = \left[B_{m+1} \cdot \frac{\partial a_m}{\partial x_m} \cdot A_{m-1}\right]_{ij}, \quad m = 2, 3, \cdots, n-2, \tag{3}$$

$$\frac{\partial A_{ij}}{\partial c} = \left[\frac{\partial a_{n-1}}{\partial c} A_{n-2} + \sum_{m=2}^{n-2} B_{m+1} \cdot \frac{\partial a_m}{\partial c} \cdot A_{m-1} + B_2 \frac{\partial a_1}{\partial c}\right]_{ij}.$$

For the particular cases where $m = 1$ and $m = n - 1$, respectively, the second equation of (3) becomes

$$\frac{\partial A_{ij}}{\partial x_1} = \left[B_2 \cdot \frac{\partial a_1}{\partial x_1}\right]_{ij}$$

and

$$\frac{\partial A_{ij}}{\partial x_{n-1}} = \left[\frac{\partial a_{n-1}}{\partial x_{n-1}} \cdot A_{n-2}\right]_{ij}.$$

It is noted from (1) and (2) that in order to compute $\frac{\partial F}{\partial x_m}$ we need $\frac{\partial A_{ij}}{\partial x_m}$, and that in order to compute $\frac{\partial F}{\partial c}$ we need $\frac{\partial A_{ij}}{\partial c}$, $\frac{\partial T^*}{\partial c}$, $\frac{\partial r_{\alpha n}}{\partial c}$, $\frac{\partial r_{\beta n}}{\partial c}$ and $\frac{\partial \gamma_n}{\partial c}$. It is also noted that in order to compute $\frac{\partial F}{\partial x_n}$ and $\frac{\partial F}{\partial x_0}$, in particular, we need $\frac{\partial r_{\alpha n}}{\partial \alpha_n}$, $\frac{\partial r_{\beta n}}{\partial \beta_n}$, $\frac{\partial \gamma_n}{\partial \beta_n}$, $\frac{\partial T^*}{\partial \alpha_0}$, $\frac{\partial T^*}{\partial \rho_0}$, and $\frac{\partial T^*}{\partial d_0}$. Inasmuch as $\frac{\partial r_{\alpha n}}{\partial c}$, $\frac{\partial r_{\beta n}}{\partial c}$, $\frac{\partial \gamma_n}{\partial c}$, and terms necessary to compute $\frac{\partial F}{\partial x_n}$ and $\frac{\partial F}{\partial x_0}$ are simple to calculate, they are not discussed here.

From the above discussion, it becomes clear that in order to compute phase-velocity partial derivatives with respect to model parameters, we need only to compute $\frac{\partial (a_m)_{ij}}{\partial x_m}$, $\frac{\partial (a_m)_{ij}}{\partial c}$, and $\frac{\partial T^*}{\partial c}$. The formulae needed to compute these terms are presented in the following section.

FORMULAE

Expressions necessary to compute the phase-velocity partial derivatives are given below. These expressions should give users of the present method a convenience and saving of time required to carry through the tedious calculations. It should be noted that in the case of Rayleigh waves there are three situations in connection with the relation between the phase velocity and body-wave velocities. They are: (i) $c > \alpha_m$ and $c > \beta_m$, that is, both $r_{\alpha m}$ and $r_{\beta m}$ are positive real; (ii) $c < \alpha_m$ and $c > \beta_m$, that is, $r_{\alpha m}$ is negative pure imaginary while $r_{\beta m}$ is positive real; (iii) $c < \alpha_m$ and $c < \beta_m$, that is, both $r_{\alpha m}$ and $r_{\beta m}$ are negative pure imaginary. In the following expressions a triple sign, that is, three signs put together vertically, applies, in the order from top to bottom, to the above three cases. When the three cases have a common sign, only a single sign appears. It is also understood that whenever $r_{\alpha m}$ and $r_{\beta m}$ are purely imaginary, $r_{\alpha m}$ and $r_{\beta m}$ in the following expressions actually represent $r^*_{\alpha m}$ and $r^*_{\beta m}$, respectively; and trigonometric functions become corresponding hyperbolic functions.

Because the expressions for the elements of the layer matrix have been published previously—see Haskell (1953: 21, 30) and Harkrider (1964: eqs. 16, 25)—the expressions for only their partial derivatives are presented here. In the following expressions, Q_m stands for $kd_m\, r_{\beta m}$:

$$\frac{\partial (a_m)_{11}}{\partial \alpha_m} = \begin{smallmatrix}-\\+\\+\end{smallmatrix} \frac{c\,\omega\, d_m\, \gamma_m \sin P_m}{\alpha_m^3\, r_{\alpha m}};$$

$$\frac{\partial (a_m)_{11}}{\partial \beta_m} = \frac{4\beta_m}{c^2}(\cos P_m - \cos Q_m) - \frac{c\,\omega\, d_m\,(\gamma_m - 1)\sin Q_m}{\beta_m^3\, r_{\beta m}} \;;$$

$$\frac{\partial (a_m)_{11}}{\partial \rho_m} = 0 \;;$$

$$\frac{\partial (a_m)_{11}}{\partial d_m} = \mathrm{k}\Big[\overset{-}{\underset{+}{+}}\gamma_m\, r_{\alpha m} \sin \mathrm{P}_m \overset{+}{\underset{-}{+}} (\gamma_m - 1)\, r_{\beta m} \sin \mathrm{Q}_m\Big] ;$$

$$\frac{\partial (a_m)_{11}}{\partial c} = -\,\frac{1}{c}\Big[2\gamma_m\, (\cos \mathrm{P}_m - \cos \mathrm{Q}_m) + \frac{1}{r_{\alpha m}\, r_{\beta m}}$$

$$\{\gamma_m\, \mathrm{Q}_m \sin \mathrm{P}_m - (\gamma_m - 1)\, \mathrm{P}_m \sin \mathrm{Q}_m\}\Big] ;$$

$$\frac{\partial (a_m)_{12}}{\partial \alpha_m} = \overset{-}{\underset{+}{+}}\, i\, \frac{c^2\, (\gamma_m - 1)}{\alpha_m^3\, r_{\alpha m}^3}(\mathrm{P}_m \cos \mathrm{P}_m - \sin \mathrm{P}_m) ;$$

$$\frac{\partial (a_m)_{12}}{\partial \beta_m} = 2i\Big[\,\frac{2\beta_m}{c^2}\Big(\frac{\sin \mathrm{P}_m}{r_{\alpha m}} \overset{+}{\underset{-}{+}} r_{\beta m} \sin \mathrm{Q}_m\Big) - \frac{1}{\beta_m\, r_{\beta m}}$$

$$(\sin \mathrm{Q}_m + \mathrm{Q}_m \cos \mathrm{Q}_m)\Big] ;$$

$$\frac{\partial (a_m)_{12}}{\partial \rho_m} = 0 ;$$

$$\frac{\partial (a_m)_{12}}{\partial d_m} = i\mathrm{k}\,\Big[(\gamma_m - 1) \cos \mathrm{P}_m \overset{+}{\underset{-}{+}} \gamma_m\, r_{\beta m}^2 \cos \mathrm{Q}_m\Big] ;$$

$$\frac{\partial (a_m)_{12}}{\partial c} = \frac{i}{c}\Big[\frac{\gamma_m - 1}{r_{\alpha m}\, (c^2 - \alpha_m^2)}(\alpha_m^2\, \mathrm{P}_m \cos \mathrm{P}_m \overset{-}{\underset{+}{+}} c^2 \sin \mathrm{P}_m)$$

$$+ \gamma_m\, \Big(\mathrm{k}\, d_m \cos \mathrm{Q}_m \overset{-}{\underset{+}{-}} 2\, r_{\beta m} \sin \mathrm{Q}_m + \frac{c^2 \sin \mathrm{Q}_m}{\beta_m^2\, r_{\beta m}} - \frac{2 \sin \mathrm{P}_m}{r_{\alpha m}}\Big)\,\Big] ;$$

$$\frac{\partial (a_m)_{13}}{\partial \alpha_m} = -\,\frac{\mathrm{k}\, d_m \sin \mathrm{P}_m}{\rho_m\, \alpha_m^3\, r_{\alpha m}} ;$$

$$\frac{\partial (a_m)_{13}}{\partial \beta_m} = \frac{\mathrm{k}\, d_m \sin \mathrm{Q}_m}{\rho_m\, \beta_m^3\, r_{\beta m}} ;$$

$$\frac{\partial (a_m)_{13}}{\partial \rho_m} = \frac{1}{c^2 \rho_m^2}\, (\cos \mathrm{P}_m - \cos \mathrm{Q}_m) ;$$

$$\frac{\partial (a_m)_{13}}{\partial d_m} = \frac{\mathrm{k}}{c^2 \rho_m}\, (\overset{+}{\underset{-}{-}}\, r_{\alpha m} \sin \mathrm{P}_m \overset{-}{\underset{+}{-}} r_{\beta m} \sin \mathrm{Q}_m) ;$$

$$\frac{\partial(a_m)_{13}}{\partial c} = \frac{1}{c^3 \rho_m}\Big[2\,(\cos \mathrm{P}_m - \cos \mathrm{Q}_m) + \frac{1}{r_{\alpha m}\, r_{\beta m}}(\mathrm{Q}_m \sin \mathrm{P}_m$$

$$- \mathrm{P}_m \sin \mathrm{Q}_m)\Big] ;$$

$$\frac{\partial(a_m)_{14}}{\partial \alpha_m} = \overset{-}{\underset{+}{+}} \frac{i}{\rho_m\, \alpha_m^3\, r^3_{\alpha m}} (\mathrm{P}_m \cos \mathrm{P}_m - \sin \mathrm{P}_m) ;$$

$$\frac{\partial(a_m)_{14}}{\partial \beta_m} = - \frac{i}{\rho_m\, \beta_m^3\, r_{\beta m}} (\sin \mathrm{Q}_m + \mathrm{Q}_m \cos \mathrm{Q}_m) ;$$

$$\frac{\partial(a_m)_{14}}{\partial \rho_m} = - \frac{i}{c^2\, \rho_m^2} \Big(\frac{\sin \mathrm{P}_m}{r_{\alpha m}} \overset{+}{\underset{-}{+}} r_{\beta m} \sin \mathrm{Q}_m\Big) ;$$

$$\frac{\partial(a_m)_{14}}{\partial d_m} = i\, \frac{\mathrm{k}}{c^2 \rho_m} (\cos \mathrm{P}_m \overset{+}{\underset{-}{+}} r^2_{\beta m} \cos \mathrm{Q}_m) ;$$

$$\frac{\partial(a_m)_{14}}{\partial c} = - \frac{i}{c^3\, \rho_m}\Big[\, 2\,\Big(\frac{\sin \mathrm{P}_m}{r_{\alpha m}} \overset{+}{\underset{-}{+}} r_{\beta m} \sin \mathrm{Q}_m\Big) \overset{-}{\underset{+}{+}} \frac{1}{r^3_{\alpha m}} \Big(\mathrm{P}_m \cos \mathrm{P}_m -$$

$$\frac{c^2 \sin \mathrm{P}_m}{\alpha_m^2}\Big) - \frac{c^2 \sin \mathrm{Q}_m}{\beta_m^2\, r_{\beta m}} - \mathrm{k}\, d_m \cos \mathrm{Q}_m\Big] ;$$

$$\frac{\partial(a_m)_{21}}{\partial \alpha_m} = i\, \frac{2\, \beta_m^2}{d_m^3\, r_{\alpha m}} (\sin \mathrm{P}_m + \mathrm{P}_m \cos \mathrm{P}_m) ;$$

$$\frac{\partial(a_m)_{21}}{\partial \beta_m} = - i \Big[\, \frac{4\, \beta_m}{c^2} \Big(\frac{\sin \mathrm{Q}_m}{r_{\beta m}} \overset{+}{\underset{-}{-}} r_{\alpha m} \sin \mathrm{P}_m\Big) \overset{+}{\underset{-}{+}} \frac{c^2\, (\gamma_m - 1)}{\beta_m^3\, r^3_{\beta m}}$$

$$(\sin \mathrm{Q}_m - \mathrm{Q}_m \cos \mathrm{Q}_m)\Big] ;$$

$$\frac{\partial(a_m)_{21}}{\partial \rho_m} = 0 ;$$

$$\frac{\partial(a_m)_{21}}{\partial d_m} = - i\mathrm{k}[(\gamma_m - 1) \cos \mathrm{Q}_m \overset{+}{\underset{-}{-}} \gamma_m\, r^2_{\alpha m} \cos \mathrm{P}_m] ;$$

$$\frac{\partial(a_m)_{21}}{\partial c} = - i \Big[\gamma_m \Big\{\frac{1}{c}(\mathrm{k}\, d_m \cos \mathrm{P}_m \overset{-}{\underset{+}{+}} 2\, r_{\alpha m} \sin \mathrm{P}_m) + \frac{\mathrm{c} \sin \mathrm{P}_m}{\alpha_m^2\, r_{\alpha m}}\Big\}$$

$$- \frac{2\, \gamma_m \sin \mathrm{Q}_m}{c\, r_{\beta m}} \overset{+}{\underset{-}{+}} \frac{\gamma_m - 1}{r^3_{\beta m}} \Big(\frac{\mathrm{Q}_m \cos \mathrm{Q}_m}{c} - \frac{\mathrm{c} \sin \mathrm{Q}_m}{\beta_m^2}\Big)\Big] ;$$

$$\frac{\partial(a_m)_{22}}{\partial \alpha_m} = - \frac{c^2 \mathrm{k}\, d_m (\gamma_m - 1) \sin \mathrm{P}_m}{\alpha_m^3 r_{\alpha m}} \; ;$$

$$\frac{\partial(a_m)_{22}}{\partial \beta_m} = \frac{4 \beta_m}{c^2} (\cos \mathrm{Q}_m - \cos \mathrm{P}_m) + \frac{2 \mathrm{k}\, d_m \sin \mathrm{Q}_m}{\beta_m r_{\beta m}} \; ;$$

$$\frac{\partial(a_m)_{22}}{\partial \rho_m} = 0 \; ;$$

$$\frac{\partial(a_m)_{22}}{\partial d_m} = \mathrm{k}\Big[\overset{+}{\underset{-}{-}} (\gamma_m - 1) r_{\alpha m} \sin \mathrm{P}_m \overset{-}{\underset{+}{-}} \gamma_m r_{\beta m} \sin \mathrm{Q}_m\Big] \; ;$$

$$\frac{\partial(a_m)_{22}}{\partial c} = \frac{1}{c} \Big[2 \gamma_m (\cos \mathrm{P}_m - \cos \mathrm{Q}_m) + \frac{1}{r_{\alpha m} r_{\beta m}}$$

$$\Big\{(\gamma_m - 1) \mathrm{Q}_m \sin \mathrm{P}_m - \gamma_m \mathrm{P}_m \sin \mathrm{Q}_m\Big\}\Big] \; ;$$

$$\frac{\partial(a_m)_{23}}{\partial \alpha_m} = - \frac{i}{\rho_m \alpha_m^3 r_{\alpha m}} (\sin \mathrm{P}_m + \mathrm{P}_m \cos \mathrm{P}_m) \; ;$$

$$\frac{\partial(a_m)_{23}}{\partial \beta_m} = \overset{-}{\underset{+}{-}} \frac{i}{\rho_m \beta_m^3 r_{\beta m}^3} (\mathrm{Q}_m \cos \mathrm{Q}_m - \sin \mathrm{Q}_m) \; ;$$

$$\frac{\partial(a_m)_{23}}{\partial \rho_m} = \frac{i}{c^2 \rho_m^2} \Big(\overset{-}{\underset{+}{+}} r_{\alpha m} \sin \mathrm{P}_m - \frac{\sin \mathrm{Q}_m}{r_{\beta m}}\Big) \; ;$$

$$\frac{\partial(a_m)_{23}}{\partial d_m} = i \frac{\mathrm{k}}{c^2 \rho_m} \Big(\overset{+}{\underset{-}{-}} r^2_{\alpha m} \cos \mathrm{P}_m + \cos \mathrm{Q}_m\Big) \; ;$$

$$\frac{\partial(a_m)_{23}}{\partial c} = - \frac{i}{c^3 \rho_m} \Big[2 \Big(\frac{\sin \mathrm{Q}_m}{r_{\beta m}} \overset{+}{\underset{-}{-}} r_{\alpha m} \sin \mathrm{P}_m\Big) - \mathrm{k}\, d_m \cos \mathrm{P}_m -$$

$$\frac{c^2 \sin \mathrm{P}_m}{\alpha_m^2 r_{\alpha m}} \overset{-}{\underset{+}{-}} \frac{1}{r_{\beta m}^3} \Big(\mathrm{Q}_m \cos \mathrm{Q}_m - \frac{c^2 \sin \mathrm{Q}_m}{\beta_m^2}\Big)\Big] \; ;$$

$$\frac{\partial(a_m)_{31}}{\partial \alpha_m} = \frac{c^4 \rho_m \mathrm{k}\, d_m \gamma_m (\gamma_m - 1) \sin \mathrm{P}_m}{\alpha_m^3 r_{\alpha m}} \; ;$$

$$\frac{\partial(a_m)_{31}}{\partial\beta_m} = 2\ \rho_m\Big[2\ \beta_m\ (2\ \gamma_m{-}1)\ (\cos \mathrm{P}_m - \cos \mathrm{Q}_m)$$

$$- \frac{c^2\ (\gamma_m{-}1)\ \mathrm{k}\ d_m \sin \mathrm{Q}_m}{\beta_m\ r_{\beta m}}\Big]\ ;$$

$$\frac{\partial(a_m)_{31}}{\partial\rho_m} = 2\ \beta_m^2\ (\gamma_m{-}1)\ (\cos \mathrm{P}_m - \cos \mathrm{Q}_m)\ ;$$

$$\frac{\partial(a_m)_{31}}{\partial d_m} = 2\ \mathrm{k}\ \rho_m\ \beta_m^2\ (\gamma_m{-}1)\ \Big(\underset{+}{\overset{-}{+}}\ r_{\alpha m} \sin \mathrm{P}_m \underset{-}{\overset{+}{+}}\ r_{\beta m} \sin \mathrm{Q}_m\Big)\ ;$$

$$\frac{\partial(a_m)_{31}}{\partial c} = c\ \rho_m\ \gamma_m\ \Big[2\ \gamma_m\ (\cos \mathrm{Q}_m - \cos \mathrm{P}_m) + \frac{\gamma_m{-}1}{r_{\alpha m}\ r_{\beta m}}(\mathrm{P}_m \sin \mathrm{Q}_m$$

$$- \mathrm{Q}_m \sin \mathrm{P}_m)\Big]\ ;$$

$$\frac{\partial(a_m)_{32}}{\partial\alpha_m} = \underset{-}{\overset{+}{-}}\ i\ \frac{c^4\ \rho_m\ (\gamma_m{-}1)^2}{\alpha_m^3\ r_{\alpha m}^3}\ (\sin \mathrm{P}_m - \mathrm{P}_m \cos \mathrm{P}_m)\ ;$$

$$\frac{\partial(a_m)_{32}}{\partial\beta_m} = i\ 4\ \rho_m\ \beta_m\ \Big[2\Big\{\ \frac{(\gamma_m{-}1) \sin \mathrm{P}_m}{r_{\alpha m}} \underset{-}{\overset{+}{+}}\ \gamma_m\ r_{\beta m} \sin \mathrm{Q}_m\Big\} - \frac{1}{r_{\beta m}}$$

$$(\sin \mathrm{Q}_m + \mathrm{Q}_m \cos \mathrm{Q}_m)\Big]\ ;$$

$$\frac{\partial(a_m)_{32}}{\partial\rho_m} = i\ c^2\ \Big[\ \frac{(\gamma_m{-}1)^2 \sin \mathrm{P}_m}{r_{\alpha m}}\ \underset{-}{\overset{+}{+}}\ \gamma_m^2\ r_{\beta m} \sin \mathrm{Q}_m\Big]\ ;$$

$$\frac{\partial(a_m)_{32}}{\partial d_m} = i\ \mathrm{k}\ c^2\ \rho_m\ \Big[(\gamma_m{-}1)^2 \cos \mathrm{P}_m \underset{-}{\overset{+}{+}}\ \gamma_m^2\ r_{\beta m}^2 \cos \mathrm{Q}_m\Big]\ ;$$

$$\frac{\partial(a_m)_{32}}{\partial c} = -\ i\ \rho_m\ \Big[\ \frac{c}{r_{\alpha m}}\ \Big\{2\ (\gamma_m^2{-}1) \sin \mathrm{P}_m \underset{+}{\overset{-}{+}}\ \frac{(\gamma_m{-}1)^2}{r_{\alpha m}^2}\ \Big(\mathrm{P}_m \cos \mathrm{P}_m -$$

$$\frac{c^2 \sin \mathrm{P}_m}{\alpha_m^2}\ \Big)\Big\} \underset{-}{\overset{+}{+}} \frac{4\beta_m^2}{c}\ \Big(\gamma_m\ r_{\beta m} \sin \mathrm{Q}_m \underset{+}{\overset{-}{-}} \frac{\sin \mathrm{Q}_m}{r_{\beta m}}\Big)$$

$$-\ \omega\ d_m\ \gamma_m^2 \cos \mathrm{Q}_m\Big]\ ;$$

$$\frac{\partial(a_m)_{41}}{\partial\alpha_m} = -\ i\ \frac{4\ \rho_m\ \beta_m^4}{\alpha_m^3\ r_{\alpha m}}\ (\sin \mathrm{P}_m + \mathrm{P}_m \cos \mathrm{P}_m)\ ;$$

$$\frac{\partial(a_m)_{41}}{\partial\beta_m} = i\,c^2\rho_m \Big[\frac{8\,\beta_m}{c^2}\,\Big\{\frac{(\gamma_m-1)\sin Q_m}{r_{\beta m}} \pm \gamma_m\, r_{\alpha m} \sin P_m\Big\}$$

$$\pm \frac{c^2(\gamma_m-1)^2}{\beta_m^3\, r_{\beta m}^3}(\sin Q_m - Q_m \cos Q_m)\Big] ;$$

$$\frac{\partial(a_m)_{41}}{\partial\rho_m} = i\,c^2 \Big[\frac{(\gamma_m-1)^2 \sin Q_m}{r_{\beta m}} \pm \gamma_m^2\, r_{\alpha m} \sin P_m\Big] ;$$

$$\frac{\partial(a_m)_{41}}{\partial d_m} = i\,\mathrm{k}\,c^2\,\rho_m \Big[(\gamma_m-1)^2 \cos Q_m \pm \gamma_m{}^2\, r_{\alpha m}^2 \cos P_m\Big] ;$$

$$\frac{\partial(a_m)_{41}}{\partial c} = i\,\rho_m \Big[\omega\, d_m\, \gamma_m^2 \cos P_m \mp \frac{4\,\beta_m^2}{c}\Big(\gamma_m\, r_{\alpha m} \sin P_m \mp \frac{\beta_m^2 \sin P_m}{\alpha_m^2\, r_{\alpha m}}\Big)$$

$$-\frac{c}{r_{\beta m}}\Big\{2\,(\gamma_m^2-1)\sin Q_m \mp \frac{(\gamma_m-1)^2}{r_{\beta m}^2}\Big(Q_m \cos Q_m - \frac{\mathrm{c}^2 \sin Q_m}{\beta_m^2}\Big)\Big\}\Big] ;$$

$(a_m)_{24} = (a_m)_{13}$; $(a_m)_{33} = (a_m)_{22}$; $(a_m)_{34} = (a_m)_{12}$; $(a_m)_{42} = (a_m)_{31}$;

$(a_m)_{43} = (a_m)_{21}$; $(a_m)_{44} = (a_m)_{11}$;

$$\frac{\partial \mathrm{T}^*}{\partial c} = \frac{\rho_0}{c^2 - \alpha_0^2}\Big[\omega\, d_0\, \alpha_0^2 \sec^2 \mathrm{P}_0 + \frac{c\,(c^2 - 2\,\alpha_0^2)\tan \mathrm{P}_0}{r_{\alpha 0}}\Big] .$$

Although Novotný (1970) presented the algorithm for Love waves, his paper did not provide formulae for the partial derivatives. To make this paper more useful and complete, the expressions for the partial derivatives of the elements of the Haskell layer matrix for Love waves are given below. For Love waves, the matrix equation of dispersion is:

$$\mathrm{F}(c, \omega, \beta_m, \rho_m, d_m) = \mathrm{A}_{21}^* + \rho_n \beta_n^2\, r_{\beta n}\, \mathrm{A}_{11},$$

where

$$c = c\,(\omega, \beta_m, \rho_m, d_m).$$

In the case of Love waves, we only have to consider two situations in connection with the relation between the phase velocity and shear wave velocity: (i) $c > \beta_m$ and (ii) $c < \beta_m$. A double sign, that is, two signs put together vertically applies to the above two situations.

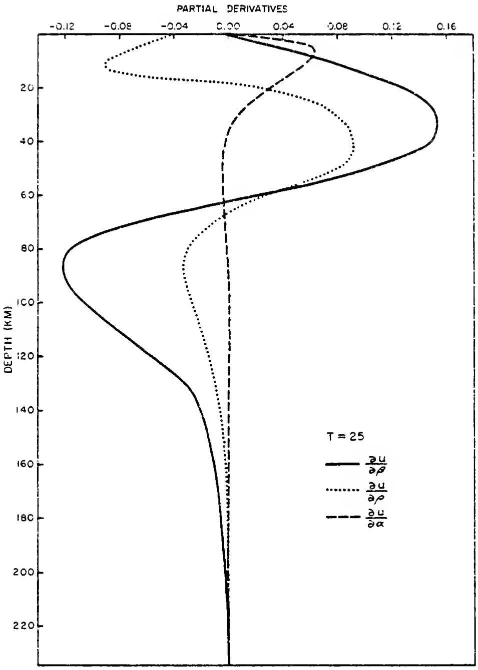

FIGURE 1.—Group velocity partial derivatives for 25-second period in the Bering Shelf.

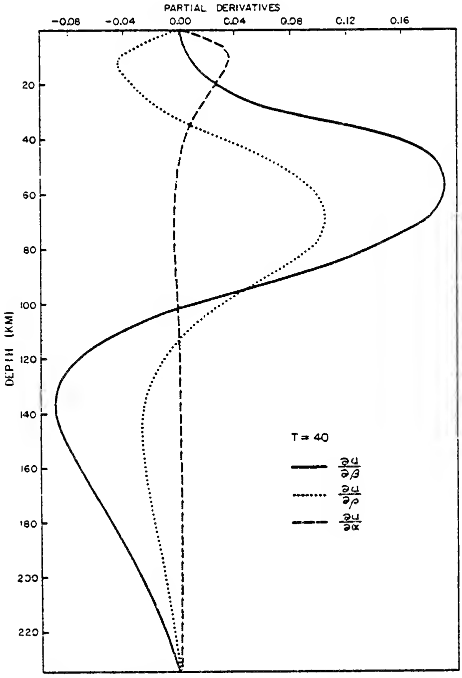

FIGURE 2.—Group velocity partial derivatives for 40-second period in the Bering Shelf.

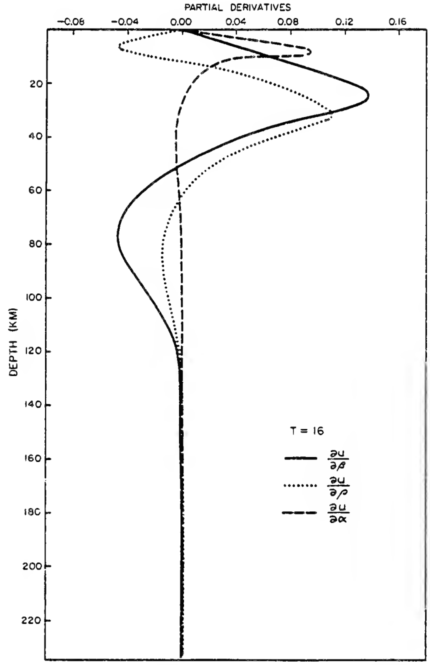

FIGURE 3.—Group velocity partial derivatives for 16-second period in the Aleutian Basin.

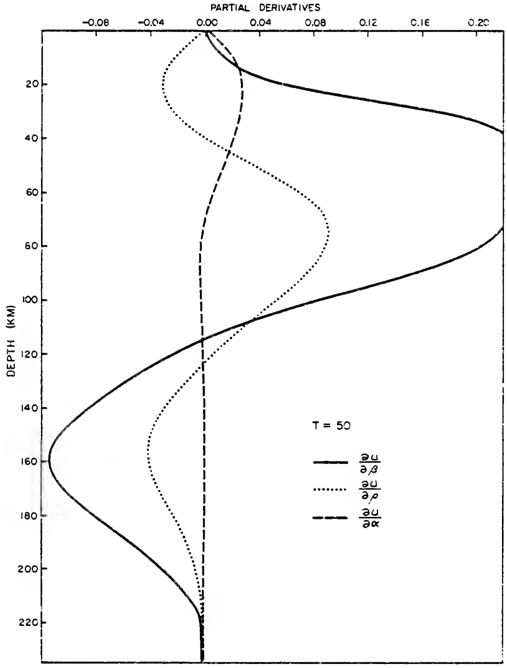

FIGURE 4.—Group velocity partial derivatives for 50-second period in the Aleutian Basin.

$$\frac{\partial(a_m)_{11}}{\partial\beta_m} = \frac{c\ \mathrm{w}\ d_m \sin \mathrm{Q}_m}{\beta_m^3\ r_{\beta m}}\ ;$$

$$\frac{\partial(a_m)_{11}}{\partial\rho_m} = 0\ ;$$

$$\frac{\partial(a_m)_{11}}{\partial d_m} = \mp\ \mathrm{k}\ r_{\beta m} \sin \mathrm{Q}_m\ ;$$

$$\frac{\partial(a_m)_{11}}{\partial c} = -\sin \mathrm{Q}_m \left[\frac{\omega\ d_m}{\beta_m^2\ r_{\beta m}} \mp \frac{\mathrm{Q}_m}{c}\right];$$

$$\frac{\partial(a_m)_{12}}{\partial\beta_m} = \mp\ \frac{i}{\rho_m\ \beta_m^5\ r_{\beta m}^3}\left[c^2\ \mathrm{Q}_m \cos \mathrm{Q}_m + \sin \mathrm{Q}_m\ (c^2 - 2\beta_m^2)\right];$$

$$\frac{\partial(a_m)_{12}}{\partial\rho_m} = -\ i\ \frac{\sin \mathrm{Q}_m}{\rho_m^2\ \beta_m^2\ r_{\beta m}}\ ;$$

$$\frac{\partial(a_m)_{12}}{\partial d_m} = i\ \frac{\mathrm{k} \cos \mathrm{Q}_m}{\rho_m\ \beta_m^2}\ ;$$

$$\frac{\partial(a_m)_{12}}{\partial c} = \frac{i}{c\ \rho_m\ \beta_m^4\ r_{\beta m}^3}\left[\mp\ c^2 \sin \mathrm{Q}_m \pm \beta_m^2\ \mathrm{Q}_m \cos \mathrm{Q}_m\right];$$

$$\frac{\partial(a_m)_{21}}{\partial\beta_m} = i\ \frac{\rho_m}{\beta_m\ r_{\beta m}}\left[(c^2 - 2\beta^2{}_m) \sin \mathrm{Q}_m - c^2\ \mathrm{Q}_m \cos \mathrm{Q}_m\right];$$

$$\frac{\partial(a_m)_{21}}{\partial\rho_m} = \pm\ i\ \beta^2{}_m\ r_{\beta m} \sin \mathrm{Q}_m\ ;$$

$$\frac{\partial(a_m)_{21}}{\partial d_m} = \pm\ i\ \mathrm{k}\ \rho_m\ \beta_m^2\ r_{\beta m}^2 \cos \mathrm{Q}_m\ ;$$

$$\frac{\partial(a_m)_{21}}{\partial c} = i\ \frac{\rho_m}{c\ r_{\beta m}}\ (c^2 \sin \mathrm{Q}_m + \beta_m^2\ \mathrm{Q}_m \cos \mathrm{Q}_m)\ ;$$

$(\mathrm{a}_m)_{22} = (\mathrm{a}_m)_{11}.$

EXAMPLES

Rayleigh-wave phase-velocity partial derivatives were computed by using the algorithm described in the section on method and the formulae in the previous section. From these phase-velocity partial derivatives, group-velocity partial derivatives were obtained by applying the method of Rodi et al. (1975) to dispersion data from the Bearing Shelf and the Aleutian Basin of the Bering Sea. Those results obtained for periods of 25 and 40 seconds in the Bering Shelf and for periods of 16 and 50 seconds in the Aleutian Basin are shown in Figures 1, 2, 3, and 4, respectively. Those readers further interested in data acquisition and earth models are referred to Jin and Herrin (1980).

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DISTRIBUTION AND HABITAT OF A NEW MAJOR CLONE OF A PARTHENOGENETIC WHIPTAIL LIZARD (GENUS *CNEMIDOPHORUS*) IN TEXAS AND MEXICO

James M. Walker
Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701

Abstract.—This report lists five localities in Val Verde, Maverick, and Webb counties, Texas, and seven in Coahuila, México, in the upper Rio Grande Valley for a new major clone (LAR-B) of a parthenogenetic whiptail lizard similar to *Cnemidophorus laredoensis*. Electrophoretic analyses indicate that all populations tested for selected gene loci are genetically identical to all-female populations discovered at nine localities in Starr, Hidalgo, and Cameron counties, Texas, and five in Tamaulipas, México, in the lower Rio Grande Valley. The paucity of locality records for LAR-B in parts of Val Verde, Kinney, Maverick, and Webb counties, and adjacent parts of Coahuila in the upper Rio Grande Valley and Cameron County and adjacent Tamaulipas in the lower Rio Grande Valley is attributable to the inaccessibility of many areas near the river. The entire range of clone LAR-B is contained within a small part of the range of the gonochoristic species *Cnemidophorus gularis*, one of the apparent progenitors of the clone. All locality records for LAR-B were found within a narrow zone of less than 10 kilometers in width on both sides of the Rio Grande between Del Rio, Val Verde County, and Palmito Hill, Cameron County (within about 16 kilometers of the Gulf of Mexico). The major habitats occupied by LAR-B in the upper Rio Grande Valley include bunchgrass-weed associations, ecotones between desert scrub and bunchgrass-mesquite, and bunchgrass/weed-mesquite, and in the lower Rio Grande Valley tall or short bunchgrass-weed mixtures, ecotones between thorn shrub and cultivated land, sandy banks along the Rio Grande, and ecotones between mixed forest and bunchgrass/weed-mesquite habitats. Parthenogenesis, in which each individual is a potential founder of a new colony, provides an adaptive reproductive mechanism for the survivor-pioneer responses that are more effective than in gonochoristic populations in those habitats that are subject to major, often catastrophic, changes. *Key words*: *Cnemidophorus*; parthenogenesis; clones; distribution; ecology; lizards of Texas and México.

Between 1983 and 1987, an investigation of the distribution and habitats of parthenogenetic whiptail lizards (genus *Cnemidophorus*) was conducted in the Rio Grande Valley and surrounding areas of Texas and México between Langtry, Val Verde County, and the Gulf of Mexico. The form (LAR-A) described as *Cnemidophorus laredoensis* by McKinney et al. (1973) was reported from 23 additional localities in Dimmit, LaSalle, Webb, Zapata, Starr, and Hidalgo counties, Texas, and 11 in Tamaulipas, México, by Walker (1987a). Also included were observations on habitats occupied by LAR-A, and on the ecological relationship of the parthenoform to its maternal progenitor *Cnemidophorus gularis*.

In August 1984, a different parthenogenetic *Cnemidophorus* (LAR-B) was discovered near the Rio Grande in Bentsen-Rio Grande Valley State Park, Hidalgo County, Texas. Clone LAR-B subsequently was found at

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localities in Starr, Hidalgo, and Cameron counties, and in Tamaulipas, including some sites where it is syntopic with LAR-A, *C. gularis*, or both. In August and September 1984, populations of parthenogenetic *Cnemidophorus* also were discovered near the Rio Grande in Val Verde County, Maverick County, and Coahuila, Mēxico, and in northern Webb County in May 1987. Electrophoretic analyses indicate that all populations tested at selected gene loci are genetically identical to LAR-B in the lower Rio Grande Valley (E. D. Parker, Jr., J. M. Walker, E. M. Niklasson, S. E. Trauth, L. J. Lester, and J. E. Cordes, unpublished data). The purpose of this paper is to present data on geographic distribution, habitats, and syntopic relationships of this newly discovered clone of *Cnemidophorus* from many areas of Texas and Mēxico where all-female populations have not been reported previously.

METHODS

Field observations in the Rio Grande Valley were made during 12 field expeditions from 1983 through 1987. Data on activity periods of lizards, soil characteristics, dominant plant forms, and general habitat quality were recorded at each locality. The term "catastrophic alteration" is used in reference to major destructive changes by human intervention (for example, fire, earth-grading, cultivation). The following geographic designations are used: 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); 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 river in Dimmit, LaSalle, and Starr counties); and lower Rio Grande Valley (within 10 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 are deposited in the University of Kansas Museum of Natural History (KU), and University of Arkansas Department of Zoology (UADZ). The coded localities and specimens of *Cnemidophorus* from each are listed in Results and Discussion.

IDENTIFICATION

The formal binomial *Cnemidophorus laredoensis* will not be further used in this report. Rather, I employ the system of informal designations of cloned hybrid populations of *Cnemidophorus* proposed by Walker (1986). Apomictic *Cnemidophorus* populations of hybrid origin are not biological species by objective definition. The level of morphological and color and pattern differentiation between clones LAR-B and LAR-A, however, exceeds that between many other all-female populations that have been described as "species" (McCoy and Maslin, 1962; Lowe and Wright, 1964; Wright and Lowe, 1965; Wright, 1967; Scudday, 1973).

LAR-B, LAR-A, and *C. gularis*, which are superficially similar, are distinguishable by distinctive features of the dorsal pattern, ventral body and tail coloration, and postantebrachial scales (Fig. 1; Table 1). Furthermore, LAR-B and LAR-A are interclonally differentiated in granules separating the paravertebral stripes, percent of the granules around midbody lying between the paravertebral stripes, numbers of granules around midbody, granules from occiput to rump, and other characters (Table 2).

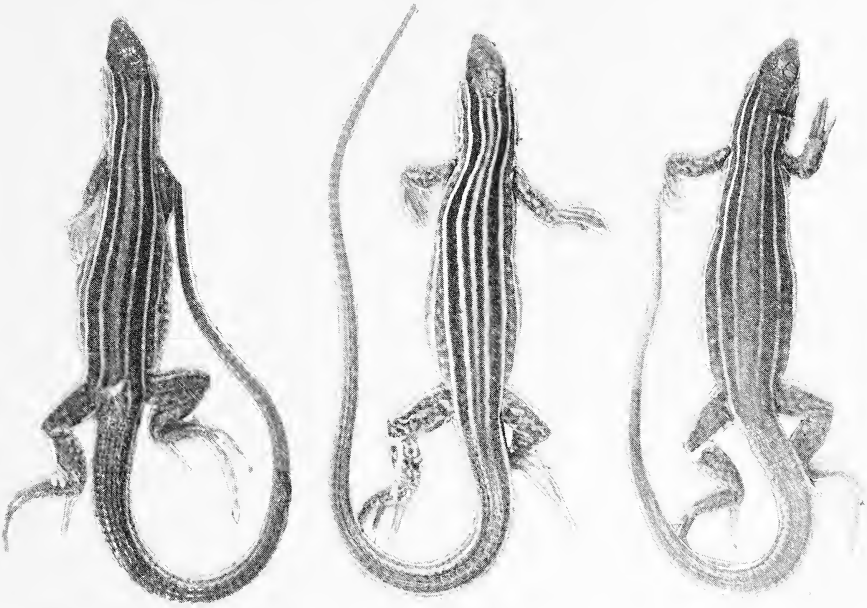

FIGURE 1. Representative specimens of LAR-B (♀♀, 80 mm), LAR-A (♀♀, 77 mm), and female *Cnemidophorus gularis* (♀♂, 75 mm) from La Grulla (site 1), Starr County (S-8*$^{+}$).

RESULTS AND DISCUSSION

More than 100 sites have been searched for the presence of LAR clones. Collection records are presented here in geographical sequence from north-northwest to south-southeast by county in Texas and by state in México. The codes for each locality are consistent with those introduced by Walker (1987a); they are subsequently used in text, figures, and tables. The three whiptail forms are identified in the citations as follows: clone A (♀♀, LAR-A), clone B (♀♀, LAR-B), and *C. gularis* (♀♂). Whiptail association codes are listed in Table 3. All collection records for all localities considered relevant to interpretation of the distribution and ecology of LAR-B follow (whether the clone was present or not). Characteristics of LAR-B sites are summarized in Table 4.

TEXAS (upper Rio Grande Valley). VAL VERDE COUNTY: (V-1) Langtry, site 1 overlooking Rio Grande (♀♂, KU 200126-200137); (V-2) Langtry, site 2 in town (♀♂, UADZ 1541-1562); (V-3) Comstock on U.S. Hwy. 90 (♀♂, UADZ 1563-1564); (V-4) 15 km. NW Del Rio, then 2.2 km. S U.S. Hwy. 90 (♀♂, UADZ 1143-1149); (V-5) Del Rio, W suburbs (♀♂, UADZ 1137-1138); (V-6) Del Rio, city park on San Felipe Creek (♀♂, KU 200104, UADZ 1574-1576); (V-7) Del Rio, vicinity of city industrial park (♀♂, UADZ 1140-1142); (V-8) Del Rio, industrial park behind cemetery (♀♂, UADZ 1139); (V-9) Del Rio, 4.8 km. W international bridge (♀♂, UADZ 1135-1136); (V-10^{++}) Del Rio, 0.8 km. N international bridge on west side of road (♀♀, LAR-B UADZ 1001-1002; ♀♂, KU 200113-

TABLE 1. Principal distinguishing characters for identification of the parthenogenetic clones LAR-B (♀♀) and LAR-A (♀♀) and females of the gonochoristic *Cnemidophorus gularis* (♀♂) where they are syntopic or closely parapatric in Texas and México.

Character	LAR-B (♀♀)	LAR-A (♀♀)	*Cnemidophorus gularis gularis* (♀♂)
		COLOR AND PATTERN	
Paravertebral stripes	Pale yellowish-tan	Vivid yellowish-green	Tan with yellowish cast to grayish-white
Vertebral stripe(s)	Tan with slight yellowish cast	Vivid yellowish-green	Tan to grayish-tan
Shape and number of vertebral stripe(s)	Always two irregular thinly divided	One straight and sharply defined complete or faintly interrupted	Two (usually) irregular, partly or completely divided, appearing as a band
Throat	Pearly white to sky blue (in some large adults)	Pearly white to sky blue (in some large adults)	Always suffused with orangish, pinkish, or reddish pigment
Ventral surface of body	Pearly white to sky blue (in some large adults)	Pearly white to sky blue (in some large adults)	Grayish-white to pale grayish-blue
Ventral surface of tail	Pearly greenish-white to pearly greenish-tan	Pearly greenish-white to pearly greenish-tan	Always reddish to orangish
		SCUTELLATION	
Postantebrachial scales	Moderately enlarged and essentially hexagonal	Moderately enlarged and essentially hexagonal	Greatly enlarged and platelike

TABLE 2. Data reductions for characters (= CH) of color and pattern (PV = granules between paravertebral stripes, PV/GAB = percent of granules around midbody lying between paravertebral stripes) and scutellation (GAB = granules around midbody, OR = granules from occiput to rump, FP = femoral pores combined, SDL = subdigital lamellae of the longest toe of the left pes, COS = circumorbital scales combined, LSG = lateral supraocular granules, MS, mesoptychial scales) in *Cnemidophorus laredoensis* (clones LAR-A and LAR-B) and *Cnemidophorus gularis.*

CH	LAR-B (♀♀) Upper Valley	LAR-B (♀♀) Lower Valley	LAR-A (♀♀) Pooled	*C. gularis* (♀♂) Pooled
PV	15.5 ± 0.17	15.0 ± 0.12	11.1 ± 0.06	15.5 ± 0.15
	12-21 (82)	10-17 (106)	9-14 (236)	10-21 (214)
PV/GAB	18.3 ± 0.16	18.0 ± 0.16	12.0 ± 0.07	16.9 ± 0.15
	14.6-22.8 (82)	12.1-21.2 (99)	9.6-15.4 (233)	11.2-23.0 (212)
GAB	84.8 ± 0.41	83.2 ± 0.23	91.6 ± 0.13	91.6 ± 0.39
	79-93 (82)	78-88 (99)	84-98 (234)	76-111 (212)
OR	210.0 ± 0.99	207.0 ± 0.62	227.4 ± 0.33	224.4 ± 0.9
	192-229 (80)	194-230 (91)	211-240 (225)	189-266 (198)
FP	32.9 ± 0.16	33.4 ± 0.14	32.9 ± 0.08	33.6 ± 0.15
	30-36 (79)	30-37 (98)	28-37 (227)	28-40 (210)
SDL	31.4 ± 0.11	32.0 ± 0.10	34.0 ± 0.06	31.8 ± 0.11
	28-33 (78)	30-35 (103)	32-37 (234)	28-38 (210)
COS	10.5 ± 0.14	10.3 ± 0.09	10.6 ± 0.07	14.5 ± 0.25
	8-13 (79)	9-14 (104)	8-15 (232)	8-30 (201)
LSG	12.4 ± 0.26	12.2 ± 0.19	14.7 ± 0.11	16.1 ± 0.31
	8-19 (79)	7-18 (103)	10-20 (230)	8-32 (203)
MS	16.2 ± 0.18	15.8 ± 0.12	17.4 ± 0.07	15.1 ± 0.11
	13-20 (78)	13-19 (97)	15-21 (219)	10-20 (201)

200115, UADZ 1565-1573); (V-11) Del Rio, 0.8 km. N international bridge on east side of road (♀♂, KU 200105-200112); (V-12) Val Verde Co. side of Sycamore Creek off U.S. Hwy. 277 (♀♂, KU 200116-200125). KINNEY COUNTY: (K-1) Pinto Creek off U.S. Hwy. 277 (♀♂, UADZ 1577-1579). MAVERICK COUNTY: (M-1) Eagle Pass, W suburbs (♀♂, UADZ 1152-1153); (M-2) Eagle Pass, just W international bridge near Indian huts (♀♀, LAR-B UADZ 1003-1004); (M-3^{++}) Eagle Pass, 1.6 km from traffic signal nearest international bridge (♀♀, LAR-B KU 200085-200089, UADZ 1005-1010; ♀♂, KU 200098-200103, UADZ 1150-1151); (M-4^{++}) El Indio, 30 km. S Eagle Pass near Rio Grande (♀♀, LAR-B definite field identification; ♀♂, definite field identification). WEBB COUNTY: (W-15^{++}) 96 km. N Laredo (or 79 km. S Eagle Pass) along FM 1472-1054 (= "Mines Road") (♀♀, LAR-B UADZ 2209-2212, 2217-2222; ♀♂, 2213, 2223-2231). ZAVALA COUNTY: (ZA-1) Crystal City, site 1 (♀♂, UADZ 1580); (ZA-2) Crystal City, site 2 near school (♀♂, UADZ 1581-1588).

TEXAS (lower Rio Grande Valley). STARR COUNTY: (S-4*) Garceno, S of town (♀♀, LAR-A UADZ 1446-1452, 1660-1670; ♀♂, UADZ 1619-1624, 1831-1834); (S-5) Rio Grande City, between international bridge and high school (♀♀, LAR-A KU 199968-199971, UADZ 1365-1375); (S-6^{+}) 7.2 km. E Rio Grande city, then 2 km. S U.S. Hwy. 83 near Rio Grande (♀♀, LAR-B UADZ 1500-1502; ♀♀, LAR-A UADZ 1453-1469); (S-7*$^{+}$) La Grulla, site 2 (♀♀, LAR-B UADZ 1717; ♀♀, LAR-A UADZ 1671; ♀♂, UADZ 1835-1858); (S-8*$^{+}$) La Grulla, site 1 (♀♀, LAR-B UADZ 1503-1506, 1718-1730; ♀♀, LAR-A UADZ 1470-1472, 1673-1881; ♀♂, UADZ 1614-1618, 1859-1878); (S-9*) junction Texas Hwy. 649 and 2686 (♀♀, LAR-A UADZ 1656; ♀♂, UADZ 2013-2015); (S-10*) El Sauz (♀♀, LAR-A UADZ 1657-1659; ♀♂, UADZ 1625, 1829-1830). HIDALGO COUNTY: (H-1) Los Ebanos, at ferry landing (♀♂, KU 199960-199964, 200038-200040); (H-2*) Los Ebanos, between town and

TABLE 3. Explanation of symbols associated with locality codes.

Symbol	LAR-B ♀♀		LAR-A ♀♀		*C. gularis* ♀♂
none	Present	or	Present	or	Present
*	Absent		Present		Present
$^{+}$	Present		Present		Absent
*$^{+}$	Present		Present		Present
$^{++}$	Present		Absent		Present

Rio Grande (♀♀, LAR-B UADZ 1116-1128, 1329-1345, 1379-1394, 1507-1537, 1731-1781, 1967-1993; ♀♀; LAR-A UADZ 1054-1058, 1307-1314, 1394, 1473-1499, 1682-1716, 1954-1966; ♀♂, UADZ 1176-1179, 1411, 1608-1613, 1879-1884, 2006-2012); (H-3^{+}) Bentsen-Rio Grande Valley State Park, along last 300 m. of trail to edge of Rio Grande (♀♀, LAR-B KU 199974-199999, 200017-200019, UADZ 1129-1130; ♀♀, LAR-A KU 199972-199973); (H-4^{++}) Rio Rico Road, levee along Rio Grande (♀♀, LAR-B UADZ 1782; ♀♂, UADZ 1885). CAMERON COUNTY: (C-1) 3.2 km. S Los Indios and U.S. Hwy. 281, few meters from edge of Rio Grande (♀♀, LAR-B UADZ 1396); (C-2^{++}) El Ranchito, 14.4 km. W Brownsville between U.S. Hwy. 281 and Rio Grande (♀♀, LAR-B KU 200020-200034, UADZ 1783-1796; ♀♂, KU 200049-200084, UADZ 1180-1203, 1348, 1886-1925); (C-3^{++}) Palmito Hill, 13.2 km. E Brownsville or, 16 km. W Gulf of Mexico, then 3.2 km. S Texas Hwy. 4 within 600 m. of Rio Grande (♀♀, LAR-B KU 200035-200037, UADZ 1346-1347, 1397; ♀♂, KU 200042-20048, UADZ 1358-1364, 1404-1409, 1926-1935); (C-4) 21.0 km. E Brownsville, then S Texas Hwy. 4 near Rio Grande (♀♂, UADZ 1936).

MEXICO (upper Rio Grande Valley). COAHUILA: (CO-1) Lake Amistad, vicinity of dam (♀♂, UADZ 1215-1221); (CO-2) 7.5 km. NW Ciudad Acuña off Mexico Hwy. 349 (♀♂, 1204-1214); (CO-3) Ciudad Acuña, suburbs W international bridge at site 1 (♀♀, LAR-B UADZ 1012-1030, 1291-1292); (CO-4^{++}) Ciudad Acuña, suburbs W international bridge at site 2 (♀♀, LAR-B UADZ 1264-1271; ♀♂, UADZ 1349-1350); (CO-5) Ciudad Acuña, riverfront park just SE international bridge (♀♀, LAR-B KU 200090-200095, UADZ 1011); (CO-6) 17.8 km. NW Jiménez, between Ciudad Acuña and Piedras Negras (♀♀, LAR-B UADZ 1031-1033); (CO-7) Jiménez, between Ciudad Acuña and Piedras Negras (♀♂, UADZ 1222-1226); (CO-8^{++}) Piedras Negras, W suburbs (♀♀, LAR-B UADZ 1035; ♀♂, UADZ 1227); (CO-9^{++}) Piedras Negras, W international bridge (♀♀, UADZ 1036-1041, 1272-1290; ♀♂, UADZ 1228-1234, 1351-1353); (CO-10) Piedras Negras, about 5 km. S international bridge (♀♀, LAR-B KU 200096-200097); (CO-11) Vicente, between Piedras Negras and Nuevo Laredo near Rio Grande (♀♂, UADZ 1228-1234); (CO-12) Hidalgo, NW Nuevo Laredo near Rio Grande (♀♂, UADZ 1245). NUEVO LEON: (NL-1) Colombia, off Hwy. 2 near Rio Grande (♀♂, UADZ 1246-1252).

MEXICO (lower Rio Grande Valley). TAMAULIPAS: (T-3*) Cuidad Miguel Alemán, S side of city (♀♀, LAR-A KU 199933-199934; ♀♂, KU 199965-199968); (T-4) Ciudad Miguel Alemán, N side of city near factory at site 1 (♀♀, LAR-A KU 199935-199940); (T-5*$^{+}$) Ciudad Miguel Alemán, N side of city near movie theater and baseball field at site 2 (♀♀, LAR-B one 1257; ♀♀, LAR-A UADZ 1076-1100, 1315-1326; ♀♂, UADZ 1259); (T-6^{+}) Ciudad Díaz Ordaz, ferry landing across from Los Ebanos (♀♀, LAR-B UADZ 1398, 1 live; ♀♀, LAR-A one definite field identification); (T-7*$^{+}$) Reynosa, NW international bridge in suburbs off Hwy. 59 (♀♀, LAR-B UADZ 1131; LAR-A definite field identification; ♀♂, UADZ 1261-1263); (T-8) Reynosa, NW of city off Hwy. 2 near hydroelectric complex (♀♀, LAR-A UADZ 1101); (T-9*) Reynosa, about 8 km. NW city off Hwy. 2 (♀♀ LAR-A UADZ 1102-1111; ♀♂, UADZ 1260); (T-10^{+}) Reynosa, several km. SE international bridge near canals (♀♀, LAR-B UADZ 1132; ♀♀, LAR-A UADZ 1112-1115); (T-11^{+}) Nuevo

TABLE 4. Habitat characteristics of localities where LAR-B has been collected; records are presented on the basis of geographical relationships from northwest to southeast in Texas, Coahuila, Nuevo León, and Tamaulipas. Abbreviations and symbols: letter = county or Mexican state code, number = locality code, no symbol = LAR-B (♀♀) alone, $^{+}$ = LAR-B and LAR-A (♀♀), $^{++}$ = LAR-B and *Cnemidophorus gularis* (♀♂), $^{*+}$ = LAR-B, LAR-A, and *C. gularis*, BG = bunchgrass(es), CA = cactus, WE = weeds, ME = mesquite, SF = sunflower, TS = thorn shrub, MF = mixed forest, WI = willows, 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 complex	Topographically complex	Soil type
V-10^{++}	1985	BG-WE-TS	+ to −	+	+	+ to −	−	SS, LS
M-2	1985	BG-WE	−	+	−	−	+ to −	SS, LS
M-3^{++}	1984	BG-WE-CA-ME	−	+ to −	+	+ to −	−	SS, GS
M-4^{++}	1987	BG-WE-ME	+ to −	+ to −	−	−	−	SS, LS
W-15^{++}	1987	BG-WE-ME	−	−	−	+ to −	−	SS, LS
S-6^{+}	1986	BG-WE	+ to −	+ to −	−	−	+ to −	SS, LS, GS
S-7^{*+}	1986	BG-WE, CA-ME-TS	+ to −	−	+	+ to −	−	LS, GS
S-8^{*+}	1986	BG-WE	+ to −	−	+	−	−	LS
H-2^{*+}	1984-86	BG-WE, BG-CA-TS	+ to −	+ to −	+ to −	+ to −	−	SS, LS, GS
H-3^{+}	1984-85	BG-WE, BG-CA-ME-MF	−	+	−	+ to −	−	SS, LS
H-4^{++}	1986	BG-WE	−	+ to −	−	−	+ to −	LS, GS
C-1	1985	BG-WE, WI	+ to −	−	−	−	+	SS, LS
C-2^{++}	1984-86	BG-WE, CA-ME-TS	+ to −	+ to −	+ to −	+	+ to −	LS, GS
C-3^{++}	1984-86	BG-WE, CA-ME-TS	+ to −	−	+	+	−	LS, GS
CO-3	1985	BG-ME	−	+	−	−	−	SS, GS
CO-4^{++}	1985	WE-BG-ME-TS, TS	−	+	+	+	+ to −	SS, GS
CO-5	1984-85	WE-MF	−	+	−	−	−	SS
CO-6	1985	BG-WE	−	+	−	−	−	SS, LS
CO-8^{++}	1985	BG-WE-TS	−	+	+	+	−	SS, GS
CO-9^{++}	1985	BG-WE-ME-TS	−	+	+	+ to −	−	LS, GS
CO-10	1984	WE-ME	−	+	−	−	−	SS, LS
T-5^{*+}	1985	BG-WE	−	−	−	−	−	SS
T-6^{+}	1985	BG-WE	−	+	−	−	+	LS, GS
T-7^{*+}	1985	BG-WE-ME	−	+	−	−	−	SS, GS
T-10^{+}	1985	WE-SF, CA-ME-TS	−	+ to −	+	−to +	−	LS, GS
T-11^{+}	1985	BG-WE, SF-WE	−	+	−	−	+	SS, GS

Progreso, NW international bridge (♀♀, LAR-B UADZ 1133-1134; ♀♀, LAR-A UADZ 1327-1328); (T-12) Matamoros, several sites (♀♂, UADZ 1354-1357, two uncatalogued).

No specimens of either of the LAR clones have been collected upriver from Ciudad Acuña, México (CO-1, CO-2), or Del Rio, Texas (V-1, V-2, V-3, V-4), as the river there is entrenched in a deep valley surrounded by rocky roughlands with desert shrub vegetation. However, *C. gularis* was abundant at all of these localities and *C. tigris* was present at CO-3, V-1, and V-2. Investigations between Eagle Pass and Laredo and Piedras Negras and Nuevo Laredo have been hampered by lack of access to the Rio Grande. In May 1985, sites along the river reached from Hwy. 2 in México yielded only specimens of *C. gularis* at CO-11 and CO-12 in Coahuila and NL-1 in Nuevo León. In May 1987, LAR-B was observed in syntopy with *C. gularis* near the Rio Grande at El Indio (M-4^{++}), Maverick County, and both were collected in northern Webb County 96 kilometers north of Laredo (or 49 kilometers south of the El Indio record).

Numerous visits have been made to sites in the middle Rio Grande Valley but have not resulted in the discovery of LAR-B. LAR-A occurs alone or with *C. gularis* (usually) at many sites between Laredo-Nuevo Laredo and Rio Grande City and at a few sites well away from the River in parts of Dimmit, LaSalle, and Starr counties (Fig. 2).

In the lower Rio Grande Valley, LAR-B apparently has a patchy distribution from about 7.2 km. E Rio Grande City and from Ciudad Miguel Alemán to within about 16 kilometers of the Gulf of Mexico at Palmito Hill (C-3^{++}). Most records for LAR-B are situated within a few hundred meters of the Rio Grande; no records for the clone farther than 10 kilometers from the river are known.

Conant (1975) depicted the range of *C. sexlineatus*, an apparent progenitor of the LAR clones (McKinney et al., 1973; Bickham et al., 1976; Wright et al., 1983), as extending to the Rio Grande in much of southern Texas. Intensive searches in 1986 produced no records for *C. sexlineatus* closer to the river than Bruni (66 km. E Laredo—UADZ 1538, 2018-2019) and 10.2 km. S Mirando City (53 km. E Laredo—UADZ 2020-2021), Webb County, and La Gloria (51 km. NE Rio Grande City—UADZ 2022-2023), Starr County. Although *C. sexlineatus* occurs on South Padre Island to the southern tip (UADZ 1399, 1798-1805), no sites for the species have been discovered in mainland Cameron County (only *C. gularis* was collected at the bridge at Port Isabel, about 3.2 kilometers from South Padre Island—UADZ 1400-1403). The distance between the closest records for LAR-A at S-9* and *C. sexlineatus* at La Gloria (both in Starr County; Fig. 2) is about 32 kilometers; the distance between the locality for LAR-B at C-3^{++} and *C. sexlineatus* on South Padre Island is about 20 kilometers.

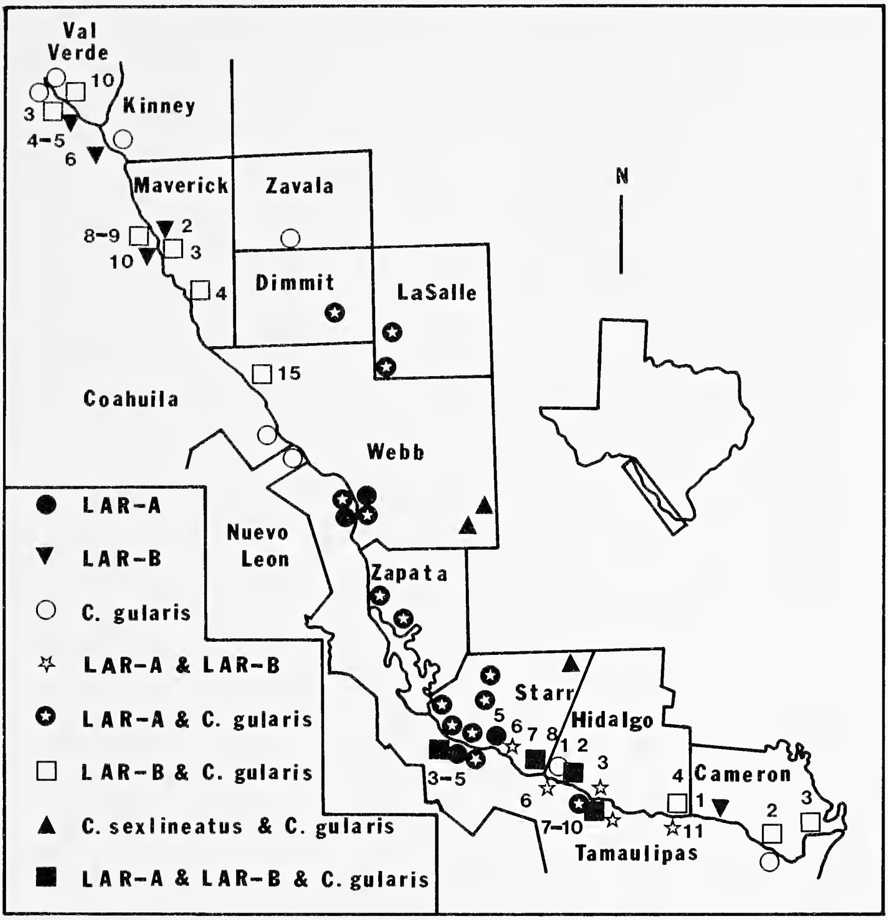

FIGURE 2. Map depicting the known ranges of the parthenogenetic clones LAR-B (♀♀) and LAR-A (♀♀) in Texas and México. Letters and numbers correspond to locality codes in text.

The entire range of LAR-B is contained within a small part of the range of the nominal subspecies of *C. gularis* (Walker, 1981a, 1981b). Syntopy between LAR-B and *C. gularis* in the upper Rio Grande Valley was observed at four sites in Texas and three in Coahuila (Table 4). LAR-B occurs in patches of altered habitat with sandy to loamy soil in Ciudad Acuña and Piedras Negras, Coahuila, where *C. gularis* frequently is absent. In the lower Rio Grande Valley, the two forms are syntopic at six sites in Texas and two in Tamaulipas. LAR-B is syntopic with both LAR-A and *C. gularis* at three localities in Texas and two in Tamaulipas (Table 4). Further efforts are expected to reveal that *C. gularis* occurs at several sites where brief visits have produced only specimens of LAR-B and LAR-A (T-6$^+$, T-10$^+$, T-11$^+$).

The zone of syntopy between LAR-B and LAR-A is on both sides of the Rio Grande from about Ciudad Miguel Alemán to Nuevo Progreso, Tamaulipas, a distance of about 90 kilometers by road.

Distributional Ecology in the Lower Rio Grande Valley

All locality records for LAR-B are in an intensively utilized region. Extensive urban, suburban, and agricultural developments have made large areas between Mission and Brownsville, Texas, unavailable to whiptails. The adjacent part of México also is extensively altered and few areas are available. The original habitats of the lower Rio Grande Valley included the following sequence of plant communities from the eastern boundary of Zapata County to the Gulf of Mexico: Chihuahuan thorn forest, upper valley flood forest, barretal, upland thorn shrub, mid-valley riparian woodland, sabal palm, and loma/tidal flats (Rio Grande Valley National Wildlife Protection Plan, Department of the Interior). Protected areas under state (Bentsen-Rio Grande Valley State Park) or federal (Santa Ana Wildlife Refuge) management, patches around cultivated land, and scattered tracts for grazing livestock provide most of the surviving examples of these formations between Rio Grande City and Brownsville.

Whether LAR-B is present or absent at a site in the lower Rio Grande Valley seems most affected by distance of the site from the river, soil characteristics, and vegetation. Whereas LAR-A is associated with sandy habitats over much of its range in Dimmit, LaSalle, Webb, Zapata, and Starr counties, and adjacent parts of Tamaulipas, all sites of syntopy between LAR-B and LAR-A in Starr County, Hidalgo County, and Tamaulipas are characterized by loamy soils with varying mixtures of sand, silt, and mud (Geologic Atlas of Texas: McAllen-Brownsville Sheet). At a typical locality for LAR-A (S-5), the presence of the clone is apparent by large numbers of burrows and tail tracks. Whereas sandy soil drains rapidly, even small amounts of rainfall can result in a quagmire at the kinds of loamy sites where LAR-B and LAR-A are syntopic (S-7^{*+}, S-8^{*+}, H-2^{*+}, T-11^{++}). Upon drying, some loamy soils develop deep cracks or become compacted; whiptail burrows and tracks are seldom apparent at such sites (Fig. 3A).

Soil characteristics (for example, texture, exposure, drainage, penetrance, origin) clearly are not as important in the distribution of *C. gularis* as they are in the distribution of LAR-B and LAR-A. *C. gularis* is successful on caliche, rock surfaces (including sandstone and granite in Oklahoma), "ersatz" substrates in Texas (including cement, asphalt, gravel), loose soils (sandy to loamy), and heavily eroded rocky to gravelly soils (Walker, 1981a, 1981b; Walker et al., 1986a; Walker and Cordes, 1988). The inability of both LAR clones to become established in areas devoid of sandy to loamy soils appears to be directly related to the absence of suitable burrowing sites (Walker et al., 1986b).

At sites of syntopy between LAR-B, LAR-A, and *C. gularis*, the relative numbers of each form can be correlated with the geographical location of the site along a northwest-southeast transect between Starr and Hidalgo counties, use of the land in the recent past (undisturbed, moderate alteration, steady degradation, catastrophic alteration), location relative to thorn shrub tracts (modified or undisturbed), and vegetation (affected by soil, exposure, successional stage). *C. gularis* inhabits all Chihuahuan thorn shrub, barretal, and upland thorn shrub climax formations bordering or entering the Rio Grande entrenchment, and from these it enters all other types of habitat available to whiptails along the river. LAR-B and LAR-A have been found only in the edge of climax formations, and always in areas where mixed forest (Fig. 3B) or bunchgrass-weed (Fig. 4A) associations form narrow ecotones with such habitats. Weedy habitats with insular characteristics (located well away from thorn shrub tracts) often support larger numbers of parthenogens than *C. gularis* (H-2^{*+}), whereas the reverse is usually true for weedy habitats adjacent to climax formations (S-7^{*+}). LAR-A reaches highest densities in predominantly bunchgrass/weed-mesquite habitats with sandy to loamy open spaces, both in near absence of *C. gularis* (T-5^{*+}) and with sizeable numbers of the species present (S-4*). LAR-B is rare (T-5^{*+}) to absent (S-4*, S-5) in bunchgrass-mesquite habitats in the lower Rio Grande Valley; the clone reaches greatest densities in riparian bunchgrass-weed habitats in old fields (H-2^{*+}, C-2^{++}) and mixed forest and bunchgrass-mesquite ecotones (H-3^{+}). The rare occurrence or absence of LAR-B upriver from S-6^{+} reflects the paucity of these habitats in the middle Rio Grande Valley.

Four sites in Starr and Hidalgo counties, each with significantly different relative numbers of LAR-B, LAR-A, and *C. gularis* were studied. At S-6^{+}, large numbers of LAR-A were found in a strip of bunchgrass-weed habitat a few meters in width along the Rio Grande, the adjacent part of a small melon field, and part way up a small slope with buffelgrass and weeds. Of 20 lizards collected in about three hours at S-6^{+}, 17 were LAR-A and only three were LAR-B (all within 75 meters of the river). Although *C. gularis* was present in a nearby thorn shrub tract, none was collected along the river at S-6^{+}, possibly because of the patchy and disturbed character of the site.

Two sites only a few hundred meters apart near La Grulla supported quite different assemblages of whiptails. S-7^{*+} consisted of a fenced tract of heavily grazed thorn shrub beside a large overgrown field crossed by an unsurfaced road. The virtual absence of lizards in the field seemed to be directly related to the absence of suitable open spaces; the few whiptails present were found along the access road (four *C. gularis* and one LAR-A collected). As expected from the appearance of the habitat, large numbers of *C. gularis* (20 collected) and almost no parthenogens (one LAR-B and no LAR-A obtained) were present in the grazed thorn shrub tract with huge clumps of *Opuntia* scattered within the compacted loamy to gravelly soil.

Site S-8^{*+}, located only a few kilometers from S-7^{*+} consisted of a tract of land out of cultivation for several years and located between narrow borders of mixed forest-mesquite. The vegetation of the overgrown field consisted of bunchgrass mixed with tall weeds (Russian thistle, sunflower, and so forth). Totals of 25 *C. gularis*, 17 LAR-B, and 12 LAR-A were captured at S-8^{*+} in a morning and two late afternoon visits. The striking difference in the composition of the whiptail communities at S-7^{*+} and S-8^{*+} was apparently related to the friable soil and open-structured grass-weed vegetation at S-8^{*+} and their absence at S-7^{*+}. Site S-8^{*+} is near the northwestern distributional limits for LAR-B in the lower Rio Grande Valley. Northwest of S-8^{*+}, LAR-B made up only 3.7 percent (one of 27) of specimens at S-7^{*+}, 15.0 percent (three of 20) at S-6^{+}, and 2.6 percent (one of 38) at T-5^{*+}.

The most remarkable site studied was an "insular" tract a few hundred meters south of Los Ebanos, Hidalgo County (Fig. 3A). H-2^{*+} consisted of scattered mesquite, huisache, and paloverde in a riparian site with ground vines, bunchgrasses, and weeds in an old field (currently part of Los Ebanos Unit, Rio Grande Valley National Wildlife Refuge). The site, which was originally covered with mixed forest, is surrounded on three sides by cultivated land and by a border of mixed forest along the Rio Grande to the east. Remnants of thorn shrub formations with compacted gravelly soil occur above the floodplain in Los Ebanos (H-1), which is separated by several hundred meters of cultivated land from H-2^{*+}. In April 1986, whiptails were widely spread through the open-structured vegetation, along an access road, and along roads around the periphery at H-2^{*+}. In May 1986, many of the small open spaces in the overgrown field were filled with lush growths of grasses and weeds. However, many lizards still were present in areas away from the road. By mid-July 1986, the area was almost completely overgrown except for scattered open spaces along the unsurfaced roads, where lizard activity was most intense. Although H-2^{*+} initially appeared to be marginally suitable for whiptails when first visited in 1985, collecting data indicate that no other site except C-2^{++} in Cameron County supported such large numbers of whiptails. In seven visits to H-2^{*+} in 1985 and 1986, totals of 157 LAR-B, 92 LAR-A, and 23 *C. gularis* were collected out of an estimated 1000 whiptails observed.

The relative numbers of LAR-B, LAR-A, and *C. gularis* observed at H-2^{*+} are consistent with expectations developed from studies elsewhere in the lower Rio Grande Valley. The low numbers of *C. gularis* at H-2^{*+}

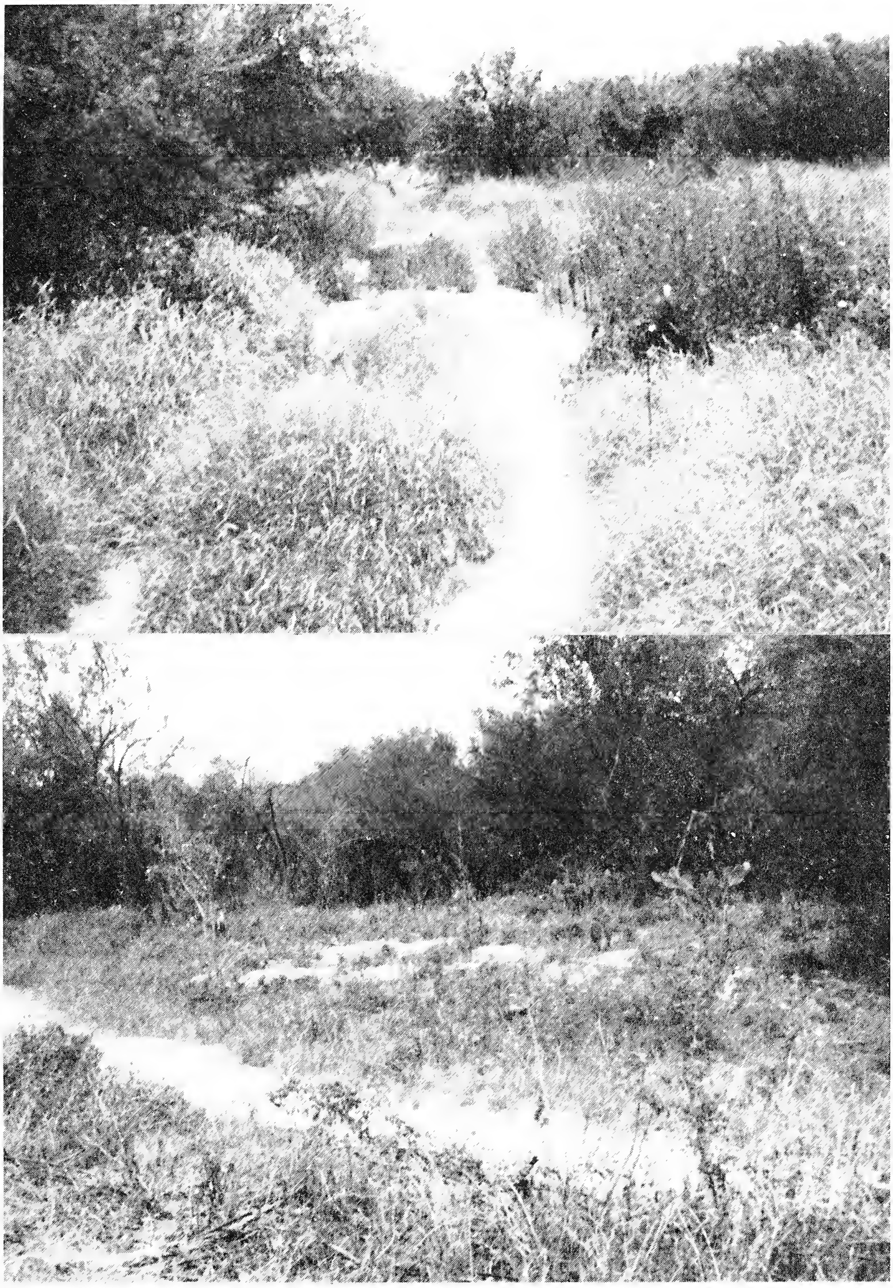

FIGURE 3. A) Example of riparian bunchgrass-weed habitat on abandoned agricultural tract at Los Ebanos, between town and Rio Grande, Hidalgo County (H-2^{*+}), which supports large numbers of LAR-B (♀♀) and LAR-A (♀♀) and a few *Cnemidophorus gularis* (♀♂). B) Example of mixed forest and bunchgrass-cactus-mesquite ecotone in Bentsen-Rio Grande Valley State Park, along last 300 meters of trail to edge of Rio Grande, Hidalgo County (H-3^{+}), which supports large numbers of LAR-B (♀♀), a few LAR-A (♀♀), and no *Cnemidophorus gularis* (♀♂).

can be attributed in part to the loamy and poorly draining qualities of the soil and the attendant riparian vegetation, but more importantly to the semi-isolated location of the tract (insular qualities) relative to thorn shrub formations about 500 meters away in Los Ebanos. Relatively large numbers of *C. gularis* and few parthenogens occur in the thorn shrub in slightly elevated areas above the valley in Los Ebanos. Although LAR-A is abundant at H-2^{*+}, the clone is significantly outnumbered by LAR-B, possibly because of soil characteristics and vegetation.

An unusual habitat for parthenogenetic whiptails was located in Bentsen-Rio Grande Valley State Park (H-3^{+}), which contains one of the few remaining tracts of subtropical forest in the lower Rio Grande Valley. In one area of the park a long nature trail winds through dense forest for about two and a half kilometers to the edge of the Rio Grande. About 300 meters from the river the trail passes through an area where bunchgrass-cactus-mesquite is thrust into the edge of the forest. Here an ecotone of a few meters in width occurs in sandy to loamy soil; numerous LAR-B were observed and collected in the open spaces along a zone of five to 10 meters on either side of the trail (Fig. 3B). LAR-B also follows footpaths well into the partly shaded, humid forest and along some areas of the steep sandy banks to the edge of the river. LAR-A enters the edge of the forest by the bunchgrass-cactus-mesquite corridor at H-3^{+}, but is apparently near the southeastern limits of its distribution on the Texas side of the Rio Grande (no specimens of LAR-A have been collected downriver from H-3^{+}). Here the numbers of LAR-B to LAR-A (31 to two) were essentially the reverse of the numbers of the two collected at S-6^{+} (three to 17) near the northwestern limit of LAR-B in the lower Rio Grande Valley. Although *C. gularis* occurs in the general area of the park, it was not observed or collected at H-3^{+}. The species does occur along forest paths in parts of Santa Ana Wildlife Refuge, downriver from H-3^{+}.

Few sites for LAR-B and none for LAR-A are known for Cameron County. Collections at a number of sites well removed from the river have invariably contained only specimens of *C. gularis*. A juvenile of LAR-B was taken at C-1 on a small sand bar with small willows between the Rio Grande and a steep forested incline bordering a large cultivated area. West of Brownsville at C-2^{++}, LAR-B occurs mainly in bunchgrass-weed associations varying from a few meters to 30 meters in width between the Rio Grande and pastureland, cultivated land, or patches of bunchgrass-mesquite. C-2^{++} supports one of the largest populations of *C. gularis* known for any site in the lower Rio Grande Valley, in a series of weedy habitats. LAR-B and *C. gularis* occur in about equal numbers in riparian areas along the river at C-2^{++}, however, *C. gularis* becomes more abundant away from the river as LAR-B disappears altogether in remnant thorn shrub pastureland and along roadsides between farmland

and bunchgrass-mesquite. The soil at C-2^{++} changes from friable loam near the river to compacted and gravelly away from the river. In early August 1984, LAR-B and *C. gularis* were found along well-worn trails used daily by large numbers of farm laborers (Fig. 4A). By late May 1986, however, the microhabitat at C-2^{++} had been bulldozed and the debris burned. Despite the catastrophic alteration of the habitat both LAR-B and *C. gularis* still were present in small numbers; other parts of C-2^{++} remained unaffected by the change.

The southeasternmost locality for parthenogenetic *Cnemidophorus* in the United States is located 13.2 km. E Brownsville (or about 16 kilometers from the Gulf of Mexico) at Palmito Hill. C-3^{++} consisted of a narrow wedge of thorn shrub vegetation located about 600 meters from the Rio Grande. In five visits to C-3^{++}, which was completely surrounded by cultivated land, 30 *C. gularis* and only six LAR-B have been collected. Five of the LAR-B were collected along a weedy strip between thorn shrub and a cotton field (Fig. 4B); the other specimen was taken about 300 meters from the river along a weedy roadside. A visit to C-3^{++} in late May 1986 revealed that the weedy strip near the cotton field had been removed by a cultivator; 10 *C. gularis*, but no LAR-B were collected at the site during the visit. *C. gularis*, but not LAR-B, has been located along the Rio Grande at C-3^{++}; only *C. gularis* has been collected along the river between C-3^{++} and the Gulf of Mexico (C-4).

Distributional Ecology in the Upper Rio Grande Valley

LAR-B has been located at only one of 12 sites investigated in Val Verde County, and three of four in Maverick County. In three years 11 visits to seven sites in and near Del Rio have resulted in totals of 32 *C. gularis* and only two LAR-B. In three visits to V-10^{++}, a weedy mixed shrub association along a sandy road about two kilometers from the Rio Grande, totals of three *C. gularis* (1 September 1984), two LAR-B (22 May 1985), and nine *C. gularis* (27 April 1986) were collected. It seems clear that LAR-B has a patchy distribution in Val Verde County. LAR-B was not found with *C. gularis* at a number of bunchgrass-weed sites (V-6, V-8, V-9, V-11) as might have been expected from observations of the clone in the lower Rio Grande Valley.

There is no evidence that LAR-B follows riparian corridors along tributaries of the Rio Grande into otherwise unsuitable roughlands of thorn shrub habitats. Only *C. gularis* was found in what appeared to be suitable habitat for the clone near San Felipe Creek (V-6), Sycamore Creek (V-12), and Pinto Creek (K-1).

In Maverick County, LAR-B was located alone at M-2 near sandy roads and paths bordered by tall weeds about 200 meters from the Rio Grande. LAR-B does occur in syntopy with *C. gularis* in the suburbs of Eagle Pass (M-3^{++}), about two and a half kilometers from M-2; both

FIGURE 4. A) Example of riparian bunchgrass-weed habitat bordering pastureland with thorn shrub remnants at El Ranchito, 14.4 km. W Brownsville, between U.S. Hwy. 281 and Rio Grande, Cameron County (C-2^{++}), which supports about a three to one ratio of *Cnemidophorus gularis* (♀♂) over LAR-B (♀♀). B) Example of weedy strip between cotton field and thorn shrub habitat at Palmito Hill, 13.2 km. E Brownsville (or 16 kilometers W Gulf of Mexico), then 3.2 kilometers S Texas Hwy. 4, within 600 meters of Rio Grande, Cameron County (C-3^{++}), which supports about a five to one ratio of *Cnemidophorus gularis* (♀♂) over LAR-B (♀♀).

FIGURE 5. A) Example of bunchgrass/weed-mesquite association at Eagle Pass, 1.6 kilometers from traffic signal nearest international bridge, Maverick County (M-3^{++}), which supports small numbers of both LAR-B (♀♀) and *Cnemidophorus gularis* (♀♂). B) Example of weedy riparian association among large trees at Ciudad Acuña, riverfront park just SE international bridge, Coahuila (CO-5), which supports a few LAR-B (♀♀) and no *Cnemidophorus gularis* (♀♂).

forms were found in August and September 1984 in degraded bunchgrass/weed-mesquite with little groundcover (Fig. 5A). Return visits to M-3^{++} in May 1985 after a relatively wet spring revealed that the mesquite had a dense groundcover of grasses and weeds that precluded successful collecting. However, six LAR-B and two *C. gularis* were collected in an adjacent open-structured bunchgrass-weed habitat. Only 13 LAR-B and 10 *C. gularis* have been collected in seven visits to four sites in Eagle Pass in 1984 and 1985.

In May 1987, the area along FM 1054-1472 between Eagle Pass, Maverick County, and Laredo, Webb County, was investigated for the first time. Both LAR-B and *C. gularis* were observed in small numbers in a patch of bunchgrass/weed-mesquite habitat near the Rio Grande at El Indio, Maverick County. South of El Indio, stops that ignored habitat characteristics such as soil and vegetation structure inevitably resulted in additional records for *C. gularis*. The presence of LAR-B in northern Webb County was established at a site (W-15^{++}) located within the northern edge of the Bigford Formation (Geologic Atlas of Texas: Crystal City-Eagle Pass Sheet). Upon approaching W-15^{++} the soil structure changed from gravelly-rocky to sandy-loamy. The surrounding country side from horizon to horizon had been cleared, resulting in verdant grazing lands. Both LAR-B and *C. gularis* were abundant in a narrow corridor of five to 10 meters from each side of the unsurfaced road to the fenced pastureland. The habitat consisted of scattered mesquite trees and acacia bushes with scattered grasses (mainly buffelgrass) and weeds. Attempts to locate LAR-B in neighboring formations with gravelly-rocky soil types proved unsuccessful, although *C. gularis* was inevitably present.

Whereas the Texas side of the river in the upper Rio Grande Valley provides few habitat opportunities for LAR-B, many areas of Ciudad Acuña and Piedras Negras, Coahuila, provide suitable habitats for the clone. In Ciudad Acuña, LAR-B initially was found in a riverfront park in a small semi-isolated patch of habitat consisting of scattered tall weeds among large trees and sandy soil thrown into rodent mounds (CO-5; Fig. 5B). No *C. gularis* were observed or collected at CO-5, possibly because of the separation of the site from climax vegetation. LAR-B was also found alone at CO-3 in a small, but densly populated, tract of degraded bunchgrass/weed-mesquite. *C. gularis* was not found at CO-3, although the species was present in an adjacent thorn shrub tract. LAR-B was located at CO-4^{++} (a few hundred meters from CO-3) with scattered individuals of *C. gularis* and a few *C. tigris* in a narrow ecotone where hilly desert scrub abutted bunchgrass-mesquite and modified thorn shrub associations near the Rio Grande.

LAR-B was found alone at one site and with *C. gularis* at two in Piedras Negras. CO-10 provides an example of a site that is subject to seasonal changes in vegetation. In early September 1984, CO-10 consisted of well-worn pathways through lush growths of Russian thistle among scattered mesquite trees. In March-early May, prior to the growth of the thistle, sites such as CO-10 have a sparse ground cover and numerous open spaces. Both sites of syntopy in Piedras Negras involved modified or degraded tracts of thorn shrub. At CO-9^{++}, LAR-B outnumbered *C. gularis* by about three to one in an area of about three city blocks with scattered thorny shrubs and mixtures of bunchgrasses and weeds. An adjacent thorn shrub tract was inhabited by *C. gularis* and a few LAR-B.

Conclusion

The patchy distribution of suitable habitats for LAR-B in the immediate vicinity of the Rio Grande apparently explains how this distinctive *Cnemidophorus* was undetected for so long. Also, relatively few museum collections exist from areas where the clone might be expected to occur, thus reducing the possibility of accidental discovery. Finally, the phenotypic similarity of LAR-B to females of *C. gularis* may have resulted in the clone not being recognized. The distribution of LAR-B is unusual among even parthenogenetic *Cnemidophorus* in the following respects: 1) intimate association with habitats in the immediate vicinity of the Rio Grande; 2) unusual shape of the range (more than 650 kilometers in length and no more than 20 kilometers in width as presently understood); 3) presence of numerous small disjunctions in the 20-kilometer zone along the river as a result of structural features relating to topography, soil type, and vegetation; 4) presence of a major disjunction in the middle Rio Grande Valley where the clone is replaced by LAR-A. But is this pattern real or is it the product of choice of collecting sites? In México, only areas within a few kilometers of the river have yielded specimens of LAR-B; all attempts to locate the form in roughland desert scrub habitats with rocky to gravelly soils have failed.

Given the intense effort to find localities for LAR-B away from the Rio Grande in Texas, which has produced only specimens of *C. gularis* and LAR-A, it seems that the clone is not widely distributed away from the river. Finally, the disjunction in the distribution of LAR-B in the middle Rio Grande Valley is correlated with the presence of the distinctive LAR-A clone at numerous sites in parts of Dimmit, LaSalle, Webb, Zapata, and Starr counties, and Tamaulipas. Inasmuch as populations of LAR-B on both sides of the disjunction are electromorphically identical at all loci tested (E. D. Parker, Jr., et al., unpublished data), the clone was apparently once distributed through the geographic hiatus.

Unlike several parthenoforms in the southwestern United States that occur in certain geographic areas not inhabited by gonochoristic congeners, LAR-B is closely associated with *C. gularis* throughout the range of the parthenoform. The distributional relationship of LAR-B to *C. gularis* at sites where only the former was observed or collected (M-2, C-1, CO-3, CO-5, CO-10) is more accurately described as narrow parapatry than an allopatry. LAR-B also is closely associated with the distinctive LAR-A clone in addition to *C. gularis* over a distance of about 90 kilometers in the lower Rio Grande Valley, a relationship that is unique to the LAR clones. The essentially riparian distribution of the LAR clones somewhat resembles the riparian distributions of *C. neomexicanus* and *C. tesselatus* (Cuellar, 1977).

The occurrence of parthenogenetic and gonochoristic species, or both, in altered or disturbed habitats has been noted by numerous workers (Walker, 1964, 1981a, 1981b, 1987a, 1987b; Wright and Lowe, 1968; Fritts, 1969; Vanzolini, 1970, 1978; Christiansen, 1971; Cuellar, 1977, 1979; Schall, 1976, 1978; Serena, 1984). All known sites for LAR-B in the upper and lower Rio Grande Valley are intensively utilized by man, and moderate to catastrophic changes have been noted between site visits (H-2^{*+}, C-2^{++}, C-3^{++}). Moreover, many sites inhabited by LAR-B in the lower Rio Grande Valley show evidence of alteration by events with catastrophic impact within the recent past (for example, fire, earth-grading, cultivation).

It is important to stress that *C. gularis* is found in weedy habitats as often as LAR-B. At many local sites, both near and away from the river, the only whiptail habitats are successional stages comprising weeds, grasses, and young shrubs. The initial impact of catastrophic or drastic alteration of habitat is not the same for LAR-B and LAR-A as for *C. gularis*. As each individual of the LAR clones is a potential founder of a new colony, parthenogenesis provides an adaptive system for the kind of "survivor-pioneer" response required for success in frequently disrupted habitats.

Although LAR-B has a restricted geographic and ecological distribution, and a significant area of disjunction in the middle Rio Grande Valley, the striking success of the clone in several types of habitats intensively used by man mitigates against regarding the form as endangered. LAR-B also reaches high population densities in Bentsen-Rio Grande Valley State Park and Los Ebanos Unit, Rio Grande Valley National Wildlife Refuge, areas that are under permanent protection.

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THE PERIPHYTIC CLADOCERA OF PONDS OF BRAZOS COUNTY, TEXAS

John M. Campbell and William J. Clark
Department of Wildlife and Fisheries Sciences, Texas A&M University
College Station, Texas 77843

Abstract.—Cladocerans living on submerged aquatic plants in the littoral zone of 20 ponds in the vicinity of Texas A&M University, Brazos Co., Texas, were sampled during an 18-month period in 1981 and 1982. The total number of periphytic cladoceran species found was 24; most were in the family Chydoridae. Survey-sampling of 20 ponds twice a year during late winter and mid-summer was adequate to provide an accurate list of the periphytic cladoceran species occurring in ponds of this region. *Key words*: Cladocera; ponds; littoral; Chydoridae; macrophytes.

Farm ponds constructed on the easily eroded clay soils in the vicinity of Texas A&M University in Brazos County, Texas, usually are characterized by high turbidity and low transparency. These ponds have narrow littoral zones with mostly floating-leaf and emergent macrophytes. Allard (1982) demonstrated that the microcrustacean community in a turbid pond had distinctive littoral as opposed to limnetic components and that the littoral species were especially abundant near beds of emergent and floating plants.

Campbell et al. (1982) devised a method for collecting the periphytic microcrustacea directly from submerged surfaces of plants, and Campbell (1983) subsequently carried out an 18-month study of littoral cladoceran population cycles in four different ponds. The study involved frequent (weekly or biweekly) sampling of the four ponds plus surveys of 16 additional ponds in the same area. As a result, a fairly complete list was obtained of the littoral cladoceran species that occur in ponds in this region. The purpose of this paper is to present 1) the inventory of periphytic cladoceran species of Brazos County identified in the Campbell (1983) study, and 2) information on the number of samples and ponds necessary to obtain a complete species list in regional studies of periphytic pond Cladocera.

Methods and Materials

The four ponds sampled frequently over the seasons—Muddy Pond (MP), Juniper Lake (JL), Wheeler Lake (WL), and College Station Central Park Road (CP)—all had well established stands of *Ludwigia peploides* (Onagraceae), a rooted plant with floating leaves and submerged stems. The ponds were all man-made and less that 20 years old. Morphometric and physico-chemical characteristics of the ponds are detailed in Table 1.

Periphytic Cladocera were collected using a hand-operated vacuum device described in Campbell et al. (1982). Replicate samples from a constant surface area of plant (10 square

TABLE 1. Morphometric and ranges of physico-chemical characteristics of the four ponds.

	Muddy Pond (MP)	Juniper Lake (JL)	Wheeler Lake (WL)	C.S.C.P. Pond (CP)
Outlet	Overflow at side of dam	Standpipe in dam	Concrete spillway	None
Surface Area (ha)	0.39	2.47	12.18	0.04
Maximum depth (m)	3.5	6.1	2.0	1.5
Water level (cm below full)	0-76	0-86	0-18	0-75
Secchi disc transparency (cm)	13-67	25-100	9-18	12-80
Turbidity (NTU)	7-25	3-17	85-95	4-13
Specific conductance (umhos)	47-56	205-230	85-104	40-67
Total alkalinity (mg/l as $CaCO_3$)	9-20	12-16	29-42	16-22
Total hardness (mg/l as $CaCO_3$)	16-20	43-58	37-40	8-18

centimeters) were collected from *Ludwigia* in each pond approximately once per week from February through November 1981, every two weeks during December and January, weekly during February 1982 and infrequently thereafter through June 1982 for a total of 52 sampling dates. On each date, 20 to 60 samples were collected from each pond.

On 9 March 1982 and 22 July 1982, five replicate samples of periphytic Cladocera were collected from the major submerged plant substrates present in the littoral zone of each of 20 different ponds, including the four ponds previously described. The ponds were all within five miles of the Texas A&M campus. Descriptions of the 16 additional ponds and the substrates sampled are in Campbell (1983).

In the laboratory, the contents of each preserved sample were washed on a fine mesh screen (no. 120) and rinsed into a petri dish. Cladocerans present in each sample were tentatively identified and counted under a dissecting microscope. Verification of species identifications were provided by Dr. David G. Frey at Indiana University. The data presented herein are records of occurrence of species in ponds on the sampling dates during 1981 and 1982. Numerical densities are reported in Campbell (1983).

RESULTS AND DISCUSSION

A total of 24 different species of periphytic Cladocera was found, with the family Chydoridae represented by 15 species (Table 2). A preponderance of chydorid species is not surprising, inasmuch as members of this group have evolved structures and behaviors for living on the surfaces of plants (Fryer, 1968). The four main ponds each contained at least four species of *Alona*, indicating that this chydorid genus is particularly well adapted to the periphytic habitat in ponds of this region.

TABLE 2. Number of dates species of periphytic Cladocera were observed in four ponds sampled at frequent intervals from February 1981 through June 1982, and frequency occurrence (number of ponds containing a species) in 20 ponds surveyed on 2 March and 22 July 1982.

		Number of dates observed				Number of ponds		
		Pond (Number of dates sampled)						March and July
Family	Species	MP (52)	JL(38)	WL(49)	CP(51)	March	July	combined
Chydoridae	*Alona affinis*	29	15	2	1	7	0	7
	Alona circumfimbriata	0	0	7	0	3	1	4
	Alona guttata	2	7	6	2	2	0	2
	Alona karua	0	0	1	13	1	3	3
	Alona monocantha	0	1	4	32	1	2	3
	Alona setulosa	33	19	48	49	7	8	11
	Alona verrucosa	13	0	0	0	0	2	2
	Alonella hamulata	12	28	45	3	7	2	7
	Chydorus brevilabris	21	34	49	36	14	14	14
	Ephemeroporous acanthodes	0	0	20	34	1	2	3
	Euryalona occidentalis	0	0	11	3	1	2	3
	Leydigia acanthocercoides	0	0	0	0	2	1	3
	Oxyurella tenuicaudis	0	0	0	1	0	0	0
	Pleuroxus denticulatus	0	0	0	0	2	3	5
	Pseudochydorus globosus	0	0	0	4	2	0	2
Daphnidae	*Ceriodaphnia quadrangula*	0	0	11	38	0	7	7
	Scapholeberis sp.	0	0	0	0	1	0	1
	Simocephalus serrulatus	35	18	29	49	16	4	17
Macrothricidae	*Ilyocryptus sordidus*	0	0	0	0	1	1	1
	Ilyocryptus spinifer	44	22	2	24	8	5	11
	Macrothrix laticornis	7	4	8	29	0	6	6
Moinidae	*Moinodaphnia macleayi*	2	0	0	0	0	1	1
Sididae	*Latonopsis occidentalis*	12	11	0	29	0	8	8
	Sida crystallina	7	20	2	0	1	0	1
Total number of species		12	11	15	16	18	18	23

Species in the family Macrothricidae are specialized for living in benthic deposits (Fryer, 1974), but occurred frequently on plants that had developed thick coatings of flocculent organic materials.

Five cladoceran species that occurred occasionally in samples from the periphytic habitat included the bosminid *Bosmina longirostris*, daphniids *Ceriodaphnia lacustris*, *Daphnia ambigua*, and *Daphnia parvula*, and the sidid *Diaphanosoma brachyurum*. These species are not listed in Table 2 because they are planktonic specialists and probably occurred on the plants by accident. *Scapholeberis* sp. is hyponeustonic (Cole, 1975) but was found in this study in association with floating leaves.

Periphytic species that occurred on many dates in at least three of the four main ponds and were widespread in the 20-pond surveys included *Alona setulosa*, *Alonella hamulata*, *Chydorus brevilabris*, *Simocephalus serrulatus*, *Ilyocryptus spinifer*, and *Latonopsis occidentalis* (Table 2). These species may be tolerant of a broad range of environmental conditions or are able to colonize and exploit new habitats quite readily, or both.

Alona affinis, *Alonella hamulata*, and *Simocephalus serrulatus* appeared to be cool-season species, occurring in more ponds during the March survey than during the survey in July. *Ceriodaphnia quadrangula*, *Macrothrix laticornis*, and *Latonopsis occidentalis* were apparently warm-season species, occurring in about one-third of the ponds during the July survey but not occurring in any ponds during the March survey. Absence of these species in samples collected during their "non-preferred" season, however, does not mean that individuals were not present in a pond. On the contrary, our observations on the reproductive strategies of these animals suggested that most species persisted through periods of stress as low-density parthenogenetic populations. Evidence of this phenomenon is discussed at length in Campbell (1983).

The total number of periphytic Cladoceran species found in the four ponds sampled intensively throughout the seasons ranged from 11 to 16 (Table 2). The average number of species per pond was 13.5. In the 20-pond surveys (both surveys combined), three of the ponds sampled contained zero or one species, but these three ponds were polluted. One received stormwater runoff directly from a major street on the Texas A&M campus; the second received poorly treated wastewater from a rural community's sewage treatment facility; and the third pond contained sediments contaminated with industrial waste.

The average number of species per pond found in each of the 20-pond surveys was 3.85 and 3.60 species in March and July, respectively. The average for the two surveys combined was 6.1 species per pond. This indicates that sampling on a single date from a pond yielded a poor estimate of the total number of species actually occurring there, which is not surprising because several periphytic cladoceran species appeared to

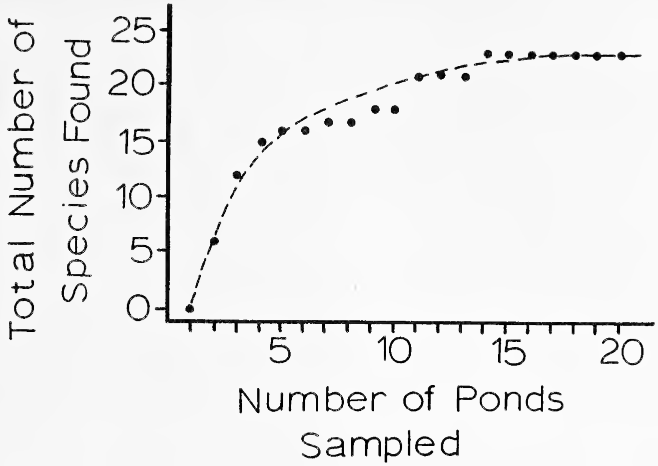

FIGURE 1. Species-pond curve showing the number of different periphytic cladoceran species accumulated from additional ponds in order as the ponds were actually sampled. The species lists were based upon five samples collected from each pond on each of two dates—2 March and 22 July 1982.

have cool- or warm-season "preferences." The average number of species per pond for the combined surveys (6.1) was much less than the average number of species per pond found with frequent sampling in the basic four-pond study (13.5) (Table 2), suggesting that sampling a pond on only two dates in two different seasons is probably not adequate to detect all of the species that occur in a particular pond.

Regardless of the inadequacy of our 20-pond surveys for characterizing the total species composition of individual ponds, we have evidence that two 20-pond surveys at different seasons provide a fairly accurate picture of the total pool of periphytic cladoceran species occurring in a particular region. A species-area curve (actually a species-pond curve) constructed for the combined March and July 20-pond surveys (Fig. 1) (with the number of species accumulated from additional ponds shown in order as the ponds were actually sampled) indicates that no additional new species were collected beyond the fourteenth pond. The only species that we know we missed in the 20-pond surveys was *Oxyurella tenuicaudis*, which was represented by only a single individual collected on one date from Central Park Pond. Therefore, we are confident that the list of periphytic cladoceran species presented in Table 2 is quite complete for this region for the time period during which the study was conducted.

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Present address of Campbell: Biology Department, Mercyhurst College, Erie, Pennsylvania 16546.

COMPARATIVE *IN VITRO* DIGESTIVE EFFICIENCY OF CATTLE, GOATS, NILGAI ANTELOPE, AND WHITE-TAILED DEER

JAMES C. PRIEBE, ROBERT D. BROWN, AND DOREEN SWAKON
Caesar Kleberg Wildlife Research Institute and College of Agriculture and Home Economics (DS), Texas A&I University, Kingsville, Texas 78363.

ABSTRACT.—The digestive efficiencies of rumen inocula from domestic cattle and goats, nilgai antelope (*Boselaphus tragocamelus*), and white-tailed deer (*Odocoileus virginianus*) were compared to test the effect of the donor ruminant species maintained on a diet of commercial wildlife pellets on *in vitro* digestion. A modification of the two-stage Tilley and Terry (1963) technique was used to evaluate their digestion of five substrates: the pelleted ration, cellulose, spiney hackberry browse (*Celtis pallida*), alfalfa hay (*Medicago sativa*), and coastal Bermada hay (*Cynodon dactylon*). The similar *in vitro* dry and organic matter digestion (IVDMD, IVOMD) across substrates of cattle (69.5 and 68.3 percent), goats (68.3 and 67.4), and nilgai (70.9 and 69.4) were greater than ($P = 0.008$, $P = 0.03$) those of deer (57.9 and 57.4). The IVDMD of the three forages by all inocula decreased as cell wall content increased, whereas *in vitro* cell wall digestion (IVCWD) did not. Overall mean IVCWD across forages of cattle (33.6), goats (33.8), and nilgai (34.6) exceeded ($P < 0.05$) those of deer (20.2). We concluded that donor ruminant species may influence *in vitro* digestion. *Key Words*: forage; digestion; cattle; goats; *Odocoileus virginianus*; *Boselaphus tragocameleus*.

One of the most perplexing problems for wildlife managers is maintaining large ruminants within the carrying capacity of the habitats they occupy. Estimating available nutrient resources facilitates solving this problem. Estimates of these resources for a given animal species depends on the production, nutrient composition, intake, and digestibility of preferred forages, and their relation to nutrient requirements of the animals. In the Texas Coastal Bend, cattle, goats, nilgai antelope (*Boselaphus tragocamelus*), and white-tailed deer (*Odocoileus virginianus*) must share habitats. Before effective management of these species can be implemented, a technique that accurately determines the nutrient availability of forages to the different species of ruminants must be found.

In vitro analysis is the standard method for estimating the *in vivo* digestibility and digestible nutrient content of forages for livestock. However, the inoculum of cattle that have been fed a hay-grain ration often is used and may not account for the fact that the natural diets consumed by these ruminants vary (Sheffield at al., 1983). While the diet of the inoculum donor is known to affect *in vitro* digestion (Bezeau, 1965; Horton et al., 1980; Campa et al., 1984), the effect of donor species is unclear. The purpose of this investigation was to compare the *in vitro* digestive efficiency of inocula from cattle, goats, nilgai and deer fed a common diet.

METHODS

Substrates

We used commercial wildlife pellets (P&M Products, San Antonio, Texas), cellulose (solka floc), spiny hackberry browse (*Celtis pallida*), alfalfa hay (*Medicago sativa*), and coastal Bermuda hay (*Cynodon dactylon*) as substrates for digestion. The three forages were selected because they are from different forage classes and provide a wide range of cell wall content (Table 1).

Duplicate samples of substrates were air dried at 60°C and ground in a Wiley mill through a one-millimeter screen. Dry matter (DM), organic matter (OM), ash, and crude protein (CP) were determined by proximate analysis (A.O.A.C., 1980). Cell wall content (CWC) was determined by the Van Soest technique (Van Soest and Wine, 1967).

Inocula Sources

Inocula from two animals of each ruminant species were used to digest substrates. All animals were maintained on a diet of commercial wildlife pellets (Wheaton and Brown, 1983). Feed and water were offered *ad libitum* for at least one month prior to inocula collection. Inocula were collected from 0800 to 1200 hours. Cattle and nilgai were sedated mildly with xylazine hydrochloride, and goats were restrained physically before inocula collection via stomach tube. White-tailed deer were sacrificed for the collection.

In Vitro Procedure

Approximately 400 milliliters of forestomach fluid was collected from each animal and transferred to a plastic jug. The jugs were placed in a beaker filled with water at 37°C, and CO_2 from a portable tank was bubbled through the contents until they reached the laboratory. Transport time ranged from five to nine minutes with a mean of 6.8 minutes.

The *in vitro* procedure was the two-stage method of Tilley and Terry (1963), as modified by Moore (Harris, 1970). Percent *in vitro* dry and organic matter digestion (IVDMD, IVOMD) were determined on all substrates for each inoculum source. Percent *in vitro* cell wall digestion (IVCWD) (Van Soest et al., 1966) was determined only on the three forages. All analyses were run in duplicate.

Statistical Methods

The results are presented in tables as percentages, but were arcsine transformed for statistical analysis. *In vitro* DM, OM, and CW digestion among ruminant species across substrates was analyzed by analysis of variance (ANOVA) for a split-plot design with repeated measures (Gill, 1978; SAS Institute, Inc., 1982). The model used was:

$$Y_{ijk} = \mu + A^{i} + D_{(i)j} + B_{k} + (AB)_{ik} + (DB)_{(i)jk},$$

Where i = 1, 2, 3, 4 ruminant species; j = 1, 2 animals per species; and k = 1, 2, 3, 4, 5 forage substrates. Tukey's studentized range (HSD) test was used to determine significant differences in IVCWD means between ruminants (SAS Institute, Inc., 1982).

RESULTS

Collection and processing times of inocula were far below the critical limits stated by Schwartz and Nagy (1972) for maintaining microbial viability. The IVDMD values of the commercial wildlife pellets by all inocula, (Table 2) were higher than those observed *in vivo* for cattle (63.3

TABLE 1. Dry matter, organic matter, ash, crude protein, and cell wall content of substrates used in *in vitro* digestibility comparison.

Substrate	DM	OM[1]	ASH[1]	CP[1]	CWC[1]
Wildlife pellets	93.3	85.1	14.9	15.7	47.5
Cellulose	95.5	99.8	0.2	0.0	99.8
Spiny hackberry	90.9	81.8	18.2	17.8	27.6
Alfalfa hay	87.7	90.4	9.6	17.1	41.0
Coastal Bermuda hay	89.2	91.5	8.5	9.1	72.4

[1] Percent of dry matter.

percent) and goats (59.1) (Swakon, unpublished data), nilgai antelope (57.0) (Priebe, 1985), and deer (54.4) (Wheaton and Brown, 1983). Pelleted diets often have a faster rate of passage *in vivo* than natural feedstuffs (Mautz and Petrides, 1971), and this reduces fermentation time and lowers digestibility (O'Dell et al., 1963).

Interspecies variation among inocula was greatest in the IVDMD and IVOMD of the cellulose substrate. Inocula that had higher cellulose digestion had greater overall digestion across substrates. Variation was contributed by substrates ($P = 0.0001$), ruminant species [IVDMD ($P = 0.008$), IVOMD ($P = 0.03$)], and substrate times ruminant species interaction [IVDMD ($P = 0.002$), IVOMD ($P = 0.003$)]. When inocula were compared across the three forage substrates only, variation due to interaction was insignificant [IVDMD ($P = 0.19$), IVOMD ($P = 0.31$)]. Substrate variation remained highly significant ($P = 0.0001$), whereas ruminant species variation was less significant [IVDMD ($P = 0.03$), IVOMD ($P = 0.08$)].

The IVDMD of the three forages by all inocula (Table 2) appeared to decrease with an increase in CWC (Table 2), whereas IVDWD seemed to be irrespective of CWC (Table 3). No statistical analyses were made with regards to these relationships because they were beyond the scope of this study. However, they agree with previous researchers (Herschberger et al. 1959; Donefer et al., 1960; Tomlin et al., 1961; Baumgardt et al. 1962; Barnes, 1967; Short et al., 1974; Robbins et al., 1975), who found that CWC greatly effect DM digestion, but not CW digestion. Specific physical and chemical properties of forage cell walls determine their degradation.

Variation in IVCWD was contributed by both forage substrate ($P = 0.001$) and ruminant species ($P = 0.006$) (Table 3). The ability of deer inoculum to digest cell walls was significantly lower ($P = 0.05$) than that of the other ruminants.

DISCUSSION AND CONCLUSIONS

Species-specific differences in the digestive efficiency of inocula can be explained on the basis of the ability of ruminal microbes to digest fiber.

Digestive physiology and ruminal microflora vary depending on forage and niche selection of ruminants (Hofmann, 1968; Gieseche and Van Goylswyk, 1975; Kay et al., 1980). Consequently, rumens of cattle, goats, and nilgai may have allowed for maintenance of greater numbers of cellulolytic bacteria than that of deer. The greater relative size of the rumen measured as the mean wet-weight of rumen contents as a percent of body weight in cattle, goats, and nilgai compared to white-tailed deer (Teer and Sheffield, 1972; Kay et al., 1980) may have allowed the digesta to be retained longer, thereby supporting a larger microbial population. *In vitro* cellulose and cell wall digestion and *in vivo* digestive efficiency comparisons of Arman and Hopcraft (1975), Huston (1976), and Mould and Robbins (1982) support this conclusion.

Discussions of the effect of donor ruminant species on *in vitro* digestion from previous research appear contradictory. Studies where no differences were found among species compared either animals with similar dietary habits (LeFevre and Kamstra, 1960; Newman, 1974) or those with varying habits on different diets (Welch et al., 1983). One exception was that of Palmer et al. (1976), but they found significant substrate-animal species interaction.

Our results generally agree with those of Short (1963), Ward (1971), Robbins et al. (1975), and Blankenship et al. (1982). Short (1963) and Robbins et al. (1975) found slight differences between cattle and deer in the *in vitro* digestion of browse. Ward (1971) reported significant differences between cattle and elk inocula in the digestion of grasses, but not in forbs and shrubs. Blankenship et al. (1982) maintained inocula donors (with the exception of deer) on a pelleted diet and found species differences in *in vitro* digestion of forages. Goat and cattle inocula were the most efficient digestors of grasses, whereas deer inoculum had the highest digestion of forbs, shrubs, and cactus. The deer were the most efficient digestor overall, but this may have been due to their maintenance diet. Interaction seemed evident in most cases, but was not tested.

In conclusion, inocula obtained from cattle, goats, and nilgai fed a pelleted ration appeared to be of similar digestive efficiency. Deer inocula seemed less efficient than other ruminant inocula, and this difference could be attributed to differences in ability to digest fiber. The species of donor animal also may affect the *in vitro* digestion of forages. The use of results acquired from inoculum of one animal species, where these factors may be different, to predict *in vivo* digestibility in another may be erroneous. Because diet selection and digestive physiology of free-ranging ruminants vary, modification of procedures used in this technique may be necessary to obtain accurate estimates. Modifications, such as the adjustment of *in vitro* fermentation time, selection of an inocula donor with similar dietary habits and digestive physiology, and maintenance of

TABLE 2.—Mean (± SE) *in vitro* dry (DMD) and organic matter digestion (OMD) percent of five substrates by inocula obtained from cattle, goats, nilgai antelope, and white-tailed deer maintained on a pelleted diet.[1]

	Substrates																							
	Pellets				Cellulose				Spiny hackberry				Alfalfa				Coastal Bermuda				$\bar{X}^3$			
Inocula[2]	DMD		OMD		DMD		OMD		DMD		OMD		DMD		OMD		DMD		OMD		DMD		OMD	
donor	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Cattle	63.4	1.6	63.0	1.3	98.6	1.4	98.1	1.4	72.2	0.6	72.5	1.0	63.1	0.1	59.2	0.7	50.3	5.3	48.6	5.0	69.5	5.4	68.3	5.6
Goats	65.6	1.4	65.9	1.5	92.1	1.0	92.3	1.0	76.1	0.5	75.3	0.4	57.7	0.0	54.2	0.4	50.0	3.8	49.1	4.7	68.3	4.9	67.4	5.2
Nilgai	65.1	0.8	63.6	1.2	98.7	0.8	97.5	1.2	76.5	0.2	76.2	1.0	65.6	0.8	62.2	1.0	48.8	0.9	47.7	1.9	70.9	5.4	69.4	5.5
Deer	56.6	4.0	58.4	2.3	65.0	10.8	63.0	16.3	66.8	0.4	67.7	0.5	58.1	1.6	55.6	1.7	43.4	0.8	42.6	1.3	57.9	3.2	57.4	3.8
$\bar{X}^4$	62.6	1.5	62.7	1.1	88.6	5.7	87.7	5.9	72.9	1.6	72.9	1.4	61.1	1.4	57.8	1.3	48.1	1.1	47.0	1.0	—		—	

[1] Significant variation contributed by substrate ($P = 0.0001$), ruminant species [IVDMD ($P = 0.008$), IVOMD ($P = 0.03$)], and substrate times ruminant species interaction [IVDMD ($P = 0.002$), IVOMD ($P = 0.003$)].

[2] Values are means of two samples from each of two animals/species.

[3] DMD and OMD averaged across substrates.

[4] DMD and OMD averaged across inocula donors.

TABLE 3. Mean (± SE) *in vitro* cell wall digestion (percent) of forage substrates by ruminant inocula donors.

Inocula donor	Forage substrate: Spiny hackberry $\bar{X}$	SE	Alfalfa $\bar{X}$	SE	Coastal Bermuda $\bar{X}$	SE	Mean[2] $\bar{X}$	SE
Cattle	34.7	1.1	23.4	2.2	42.8	1.6	33.6^a	3.6
Goats	31.9	2.8	26.6	0.6	42.8	0.1	33.8^a	3.1
Nilgai	34.2	0.4	28.2	1.0	41.2	2.4	34.6^a	2.5
Deer	21.4	4.4	13.1	5.2	26.0	5.8	20.2^b	3.3
$\bar{X}$[1]	30.6^a	2.2	22.8^b	2.5	38.2^c	2.9		

[1] Means with different letters across rows are significantly different ($P < 0.05$).

[2] Means with different letters down columns are significantly different ($P < 0.05$).

the inocula donor on a similar diet to its free-ranging counterpart, are suggested before inferences are made.

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SHALLOW-WATER OCTOCORALLIA AND RELATED SUBMARINE LITHIFICATION, SAN ANDRES ISLAND, COLOMBIA

M. John Kocurko

Department of Geology and Geophysics, Midwestern State University, Wichita Falls, Texas 76308

Abstract.—Twenty species of octocorals were collected from shallow-water environments around San Andres Island, Colombia. Most species were abundant on the leeward side of the island where terraces of limestone form suitable substrate for colony attachment. No distinction was found between faunal zonations of windward as opposed to leeward environments, but leeward specimens are noticeably larger. Colony size probably is affected primarily by water depth, wave energy, and substrate.

Specimens were identified on the basis of colony morphology and spicule types. X-ray analysis of spicule material indicates a composition of high-magnesium calcite between 5.3 and 10.7 mole percent $MgCO_3$. Octocorals are effective agents of submarine lithification and sediment binding, accomplished by the development of a holdfast. Octocorals generally may be divided into two groups, those with calcified holdfasts and those with noncalcified holdfasts. X-ray analysis of calcified holdfasts from San Andres specimens indicated a composition of aragonite. *Key words*: octocorals; San Andres Island, Colombia; lithification; holdfast.

San Andres Island is a small island-reef complex located approximately 200 kilometers east of Nicaragua (Fig. 1). The marine environments of the San Andres area can be divided into the reef complex of the eastern (windward) side, and a nonreef complex on the western (leeward) side. These environments have been studied previously by Geister (1973) and Kocurko (1972, 1974, 1977); for this investigation the marine environments have been generalized as indicated in Figure 2.

Prior to this study no published data existed on the octocorals of San Andres. A tabulation by Bayer (1961) indicated nine species of octocorals (Table 1) were collected near the island of La Providencia, approximately 80 kilometers north of San Andres.

Materials and Methods

This report is intended as a basic guide to growth forms of shallow-water octocorals in the San Andres area and to relate colony growth to submarine lithification. Twenty species have been identified from collections made between 1970 and 1980. All specimens were fixed in formaldehyde and then dried. Overall colony morphology and spicules were the basis for identifications, which have been confirmed by F. M. Bayer (personal communication, 1978). Because octocorals were not examined or collected below a water depth of 25 meters, additional species probably can be added to the faunal list presented in Table 2. Detailed systematics and descriptions are not covered completely in this report; the reader is referred to Bayer (1961) for synonymies and other more complete information on octocorals.

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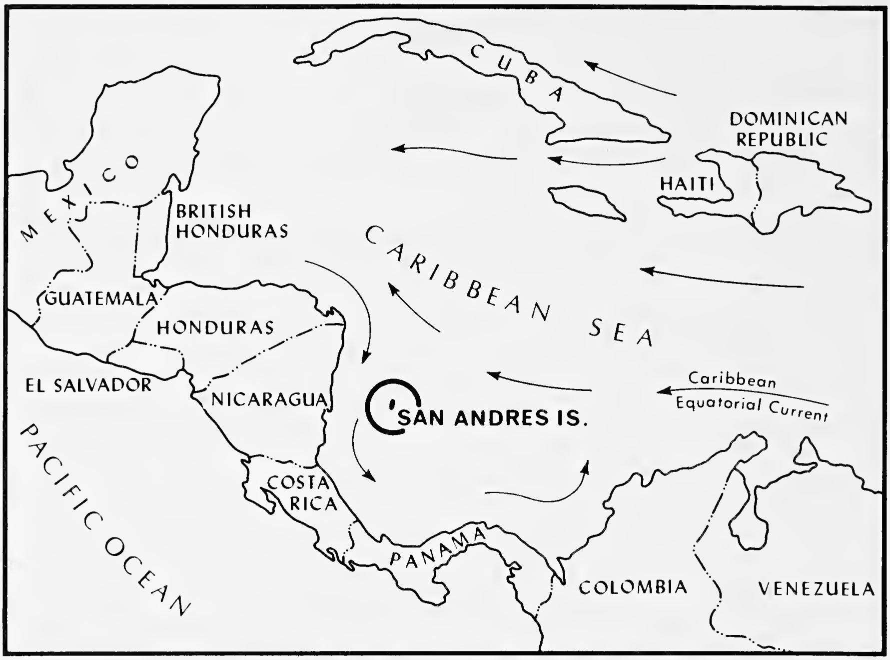


FIGURE 1. Index map of the Caribbean area.

GENERAL GROWTH ENVIRONMENT

The most prolific octocoral gardens are on the leeward side of San Andres (Fig. 2) where limestone terraces of Pleistocene age form a firm substrate to support growth (Fig. 3). In the San Andres area, octocorals usually are restricted to areas of limestone exposed on the ocean bottom (Figs. 3, 4). Rare exceptions grow in loosely packed sediment where initial attachment of the octocoral is to a small object that has been subsequently buried by sediment.

Another major controlling factor of octocoral growth is water depth. In the San Andres area, specimens from deeper water on the leeward side of the island are large and found at depths in excess of five meters. For example, *Pseudopterogorgia americana* and *P. acerosa* were particularly abundant in the deeper water of the leeward environments and may grow to heights of two meters. The same species from shallow water on the windward side were at most 75 centimeters high. The combination of shallow water depth and strong wave energy apparently dwarf many types of colonies.

Octocoral colonies found in the San Andres area had numerous commensal organisms. Many fish and crustaceans simply used the colonies as concealment, swimming around the octocoral branches. There were several noticeable associations between octocorals and invertebrates:

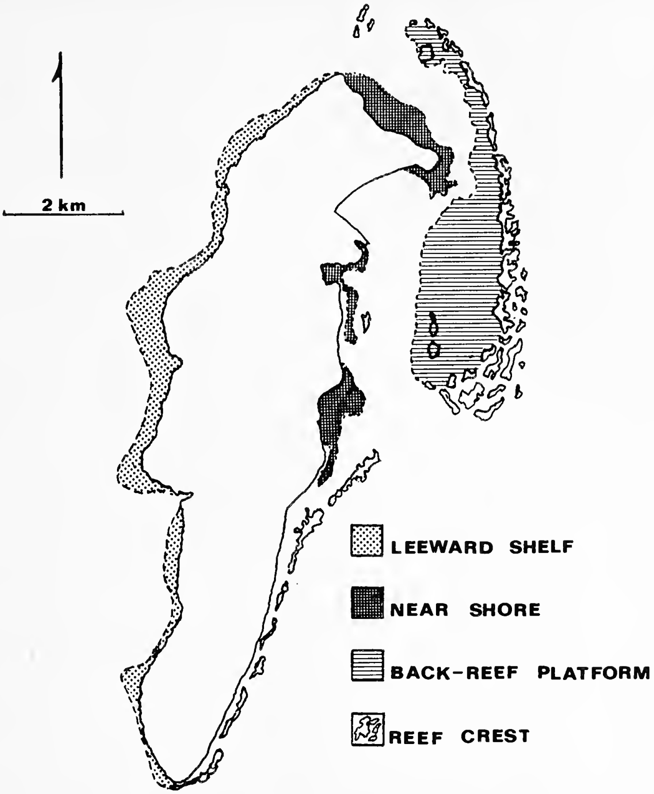


FIGURE 2. Generalized marine environments of San Andres Island.

for example, the basket-starfish, *Astrophyton*, commonly was found intwined in the branches of *Pseudopterogorgia acerosa.* No other octocoral showed a similar association. In addition to *Astrophyton*, *P. acerosa* also harbored a brittle-star, *Ophiothrix suensonii. Gorgonia*, *Plexaurella*, and *Plexaura* commonly were found with the gastropod, *Cyphoma*, grazing along their branches. The pelecypod, *Pteria*, attaches to the axial cortex of *P. acerosa.* The most apparent commensal was coralline red algae, which often encrusted the calcified base and lower stem of specific octocorals.

SEDIMENT CONTRIBUTION AND LITHIFICATION

Octocorals aid in the accumulation of sediments by baffling of suspended material and by contribution of spicules. According to Bayer (1961), based on work by Cary (1914, 1931), the average spicule content of 12 species (of octocoral) was found to be 27.4 percent of the wet weight of the colonies, and the average weight of spicules per square yard, based on 20 samples was 2.1225 pounds. Bayer noted that one ton

TABLE 1. Faunal list of specimens collected near La Providencia (after Bayer, 1961).

Briareum asbestinum
Erythropdium caribaeorum
Plexaura homomalla forma kukenthali
Plexaura flexuosa
Pseudoplexaura porosa
Eunicea mammosa
Pseudopterogorgia bipinnata
Pseudopterogorgia acerosa
Gorgonia ventalina

of limestone per acre can be released annually by gorgonians in the form of spicules.

Based on grain count analyses of sediments from San Andres, octocoral spicules make up a small percentage of sediment constituents (less than five percent). Even areas of substantial octocoral growth showed surprisingly low spicule counts from sediment. Several explanations for the general lack of spicules are available: spicules may undergo dissolution during organic decay of the colony; spicules may be redistributed by currents; and the small size of many types of spicules make their detection difficult if not impossible.

Spicule samples were analyzed by X-ray diffraction to determine mineralogy. Analyses indicated a composition of high-magnesium calcite in all species from the San Andres area. Magnesium carbonate content of the calcite ranged from 5.3 to 10.7 mole percent.

TABLE 2. Octocoral species from the San Andres Island area, Colombia. An asterisk indicates species collected with a calcified base.

Briareum asbestinum (Pallas, 1766)
**Solenopodium polyanthes* (Duchassaing and Michelotti, 1960)
**Plexaura homomalla* (Esper, 1792)
**P. flexuosa* Lamouroux, 1821
Plexaura sp.
**Pseudoplexaura porosa* (Houttuyn, 1772)
**P. wagenaari* (Stiasny, 1941)
**Eunicea mammosa* Lamouroux, 1816
Eunicea sp.
**E. tourneforti* Milne Edwards and Haime, 1857
E. calyculata (Ellis and Solander, 1786)
**Muriceopsis flavida* (Lamarck, 1815)
**Plexaurella dichotoma* (Esper, 1791)
**P. grisea* Kunze, 1916
Pseudopterogorgia bipinnata (Verrill, 1864)
P. acerosa (Pallas, 1766)
P. americana (Gmelin, 1791)
Gorgonia ventalina Linnaeus, 1758
**Pterogorgia citrina* (Esper, 1792)
**P. anceps* (Pallas, 1766)

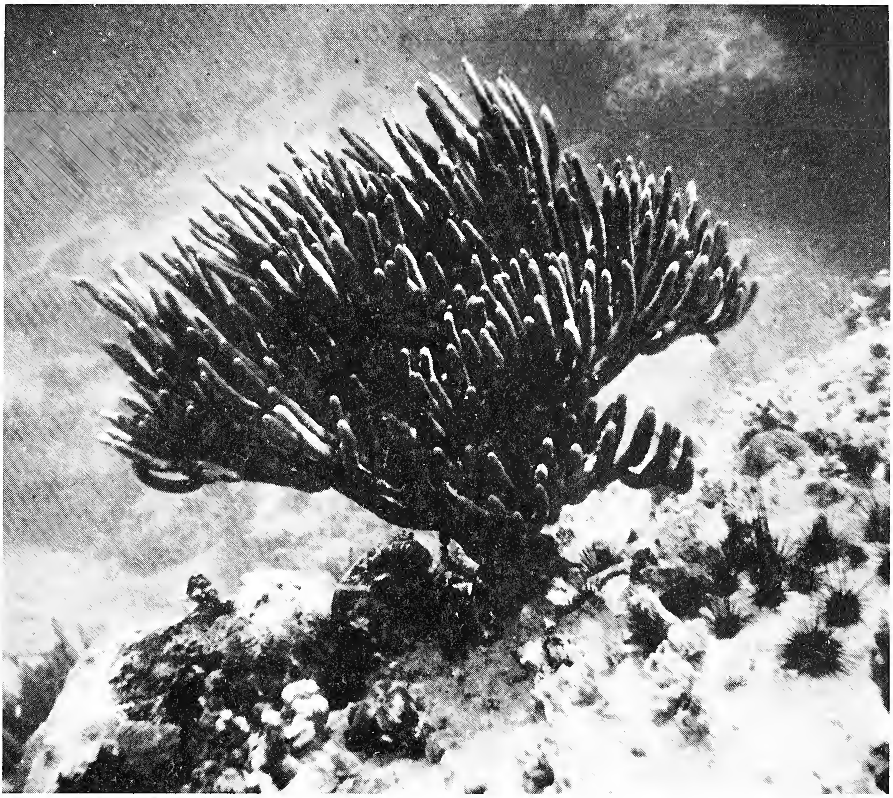


FIGURE 3. *Eunicea tourneforti* attached to a limestone cliff on the leeward shelf of San Andres Island. Colony was approximately one meter across.

Octocorals are sediment binders and are responsible for extensive submarine lithification. The basal holdfast of a colony, particularly in large specimens, has a tendency to envelop or encrust bottom material, thereby increasing the substrate volume. Holdfasts may be either calcified or noncalcified. In large colonies of both types, bases may exceed 40 centimeters in diameter, 10 to 15 centimeters in height, and 10 centimeters in thickness.

Noncalcified holdfasts generally are composed of a brownish, leathery material (gorgonin). The gorgonin is covered by an outer layer of spiculate tissue. Although little or no calcium carbonate is contributed to the substrate by this type of holdfast, it is an effective binder of bottom material and can account for considerable encrustation.

Octocorals with calcified holdfasts are most important for their contribution of calcium carbonate to the substrate. Large colonies may account for the deposition of several kilograms of carbonate material. X-ray diffraction analysis of calcified holdfasts indicates a composition of aragonite. Petrographically, the aragonite appears as a mass of

FIGURE 4. *Plexaura homomalla* attached to a loose limestone boulder.

hemispheroidal bundles of radiate aragonite needles. Each hemispheroidal feature is separated from the next by thin sheets of gorgonin. The detailed morphology of these structures has been described by Kocurko (1987).

It should be noted that a distinct difference in mineralogy exists between the spicules (high-magnesium calcite) and the holdfast (aragonite) within the same colony. As with spicules, the morphology of the hemispheroids varies from species to species. For example, *Eunicea tourneforti* has unusually large aragonite bundles exceeding 200 micrometers in width, whereas similar structures in *Plexaurella grisea* average 12 micrometers.

Calcium carbonate crystallization may be promoted by the presence of carbonate granules incorporated in the gorgonin (Szmant-Forelich, 1974) by acting as nucleation sites for crystal growth. Of the 20 species collected from the San Andres area, 12 were found to have calcified holdfasts. These species are designated by asterisks in Table 2.

In areas of extensive octocoral growth, considerable carbonate accumulation can be attributed to calcified holdfasts and recognition of these accretionary forms in the fossil record has been greatly overlooked. Attention should be drawn to the significance of early lithification by octocorals as well as their substantial contribution to substrate volume.

SYSTEMATIC DESCRIPTIONS

Subclass Octocorallia Haeckel, 1866
Order Gorgonacea Lamouroux, 1816 (emend. Verrill, 1866)
Suborder Scleraxonia Studer, 1887
Family Briareidae Gray, 1859

Briareum asbestinum (Pallas, 1766)—Plate 1, Figure 1

Specimens of this species were found in numerous environments in the San Andres area but were most common in the shallow, back-reef platform and shallow near shore. Encrustations and slender branching forms usually were found in the back-reef platform environment, near the reef crest. The clublike form was found on hard substrate near shore. Water depth was never greater than three meters. No specimens were observed on the leeward side of the island.

Similar in appearance to *Briareum asbestinum* is an octocoral identified as *Solenopodium polyanthes* (Duchassaing and Michelotti, 1860) by F. M. Bayer (personal communication, 1978). He included this species with *B. asbestinum* in his 1961 paper and, to date, has not formally separated the two. The growth form and environments closely parallel those of *Briareum*. Specimens from San Andres were collected from the back-reef side of the main reef crest. Colonies are generally small and clublike, but also may be encrusting (Plate 1, Figs. 2a, 2b, 2c).

Suborder Holaxonia Studer, 1887
Family Plexauridae Gray, 1859

Plexaura homomalla (Esper, 1791)—Plate 2, Figure 1

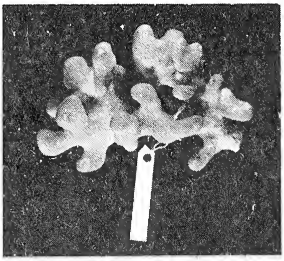
This species was found most commonly in the shallow nearshore environment on the leeward side of the island. It apparently flourishes when not exposed to strong currents or wave action. Colonies averaged 75 centimeters high and have calcified holdfasts. Specimens were observed at water depths between two and 10 meters.

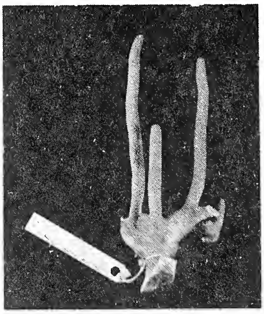
Plexaura flexuosa Lamouroux, 1821—Plate 2, Figure 2

Growth environments are the same as for *Plexaura homomalla.*

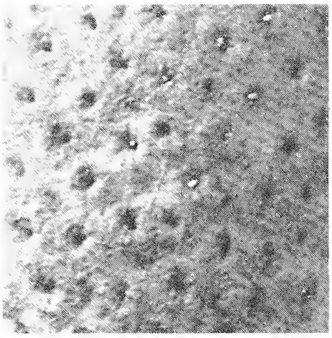
Plexaura sp.—Plate 2, Figure 3

According to F. M. Bayer (personal communication, 1978) ". . . there are several problems to be solved with the plexaurids. . . ." The figured specimen is, therefore, only tentatively identified. This specimen was collected on the leeward side of San Andres from an open shelf area at a


1a


2a


2b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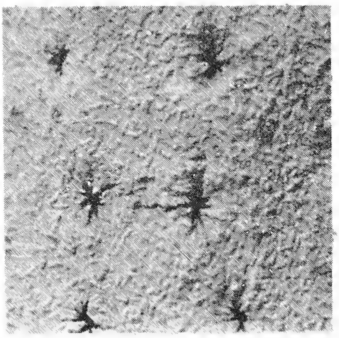
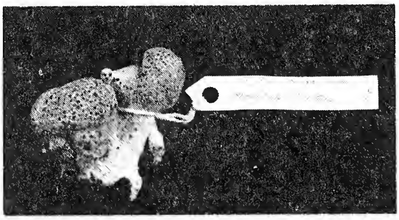

2c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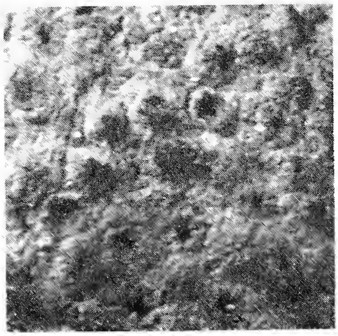
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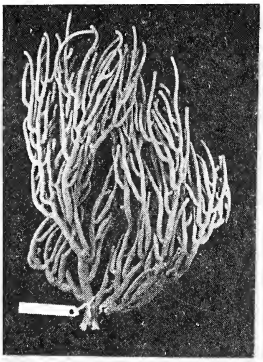
PLATE 1

FIGURE 1. *Briareum asbestinum*: 1a, label is 75 millimeters in length; 1b, × 4.1.
FIGURE 2. *Briareum asbestinum*: 2a, label is 75 millimeters in length; 2b, × 2.0; 2c, × 4.9.
FIGURE 3. *Solenopodium polyanthes*: 3a, label is 75 millimeters in length; 3b, × 3.7.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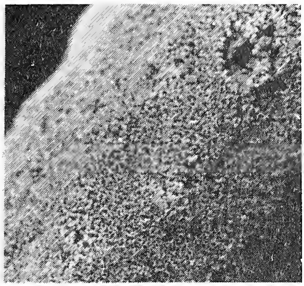
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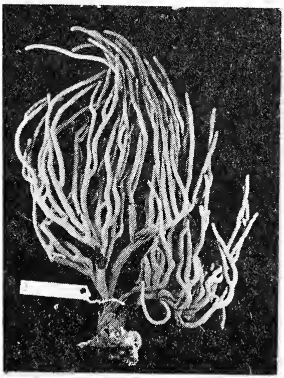
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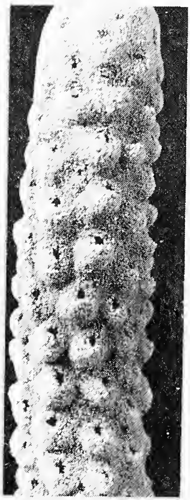
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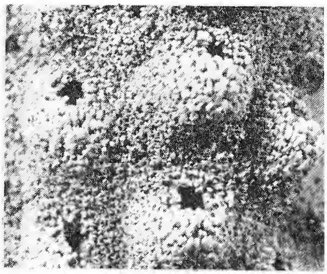
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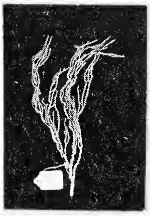
3a


3b


3c

PLATE 2

FIGURE 1. *Plexaura homomalla*: 1a, label is 75 millimeters in length. 1b × 3.7; 1c × 11.5.
FIGURE 2. *Plexaura flexuosa* 2a, label is 75 millimeters in length; 2b × 4.1; 2c × 15.5.
FIGURE 3. *Plexaura* sp.: 3a, label is 37 millimeters in length; 3b, × 4.1 3c, × 11.5.

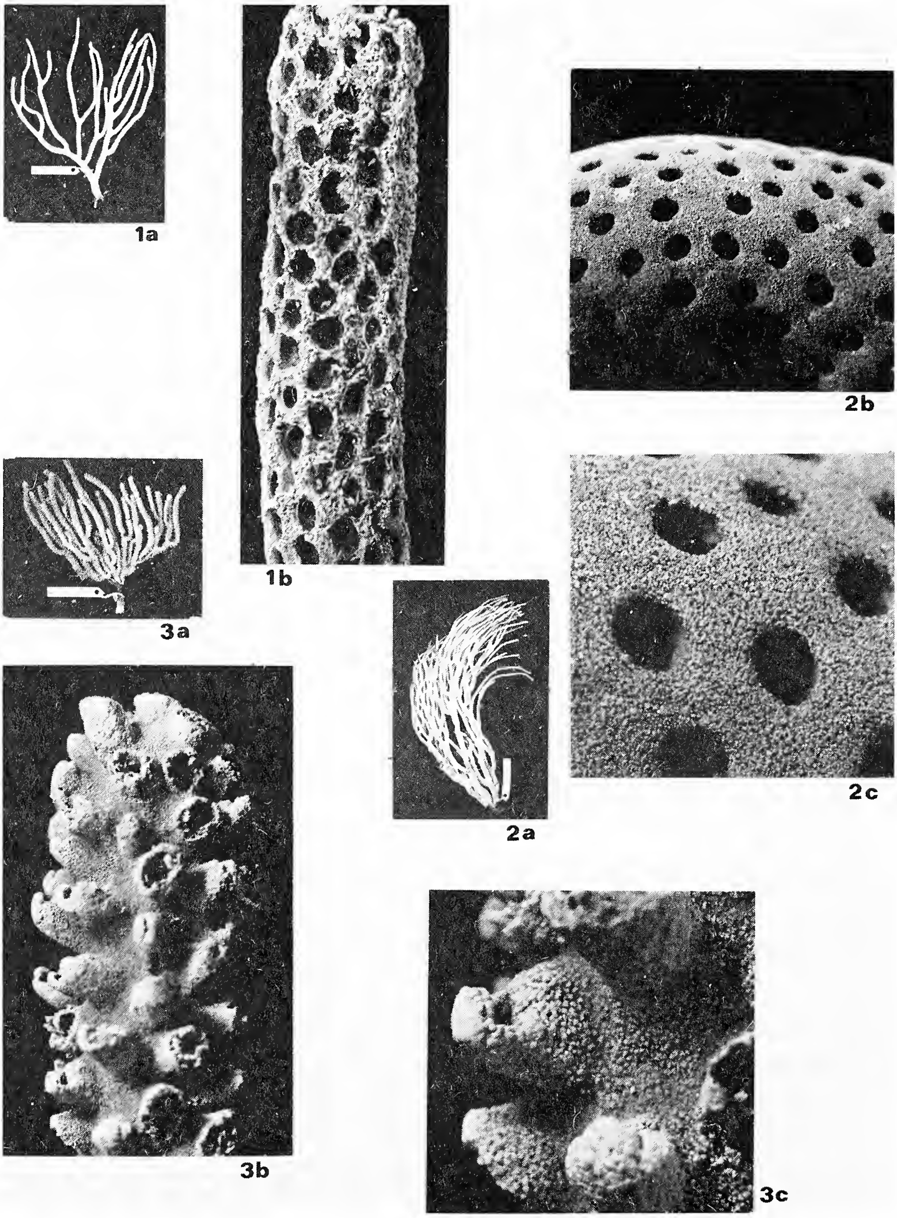

PLATE 3

FIGURE 1. *Pseudoplexaura porosa*: 1a, label is 75 millimeters in length; 1b × 3.3.

FIGURE 2. *Pseudoplexaura wagenaari* 2a, label is 75 millimeters in length; 2b, × 4.9; 2c, × 12.7.

FIGURE 3. *Eunicea mammosa*: 3a, label is 75 millimeters in length; 3b, × 3.7; 3c × 9.0.

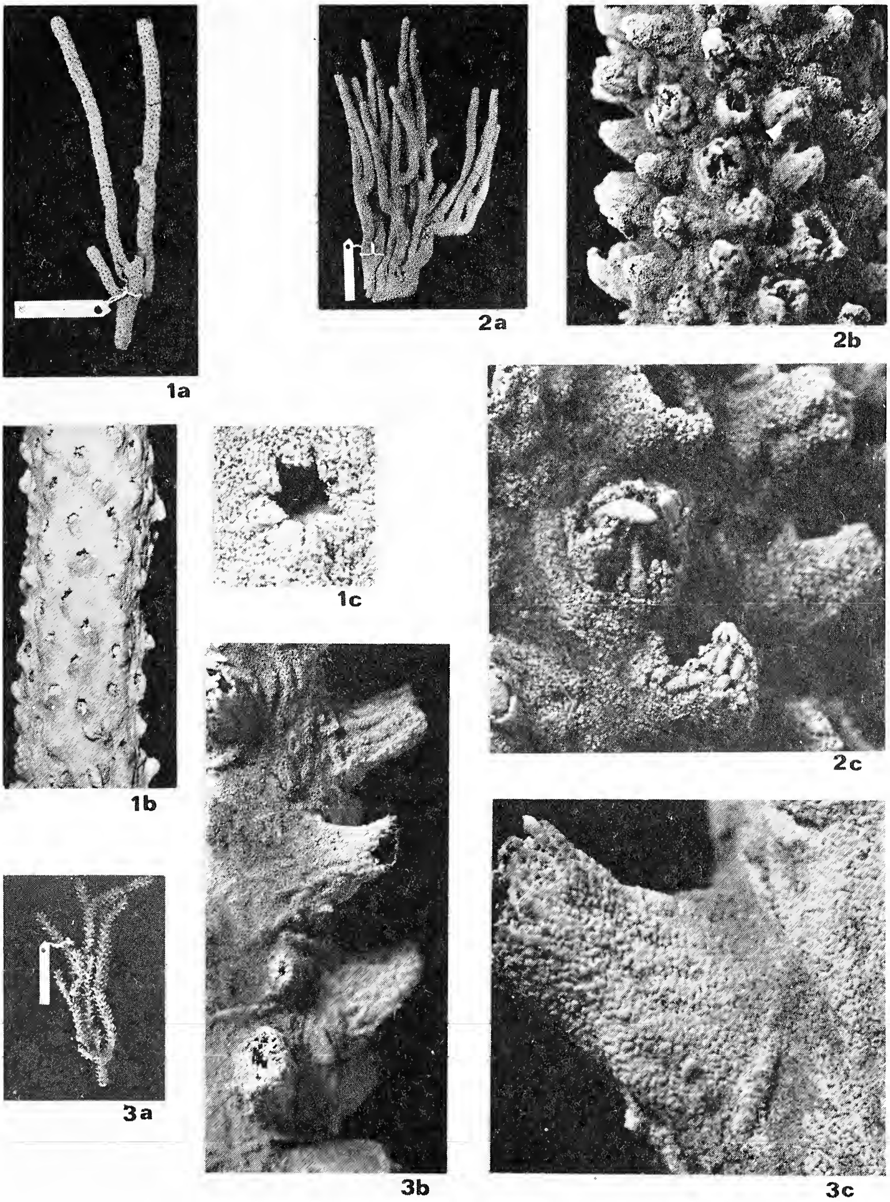

PLATE 4

FIGURE 1. *Eunicea calyculata*: 1a, label is 75 millimeters in length; 1b, × 1.6; 1c, × 8.2.
FIGURE 2. *Eunicea tourneforti*: 2a, label is 75 millimeters in length; 2b, × 2.7; 2c × 7.2.
FIGURE 3. *Eunicea* sp.: 3a, label is 75 millimeters in length; 3b, × 3.3; 3c × 9.8.

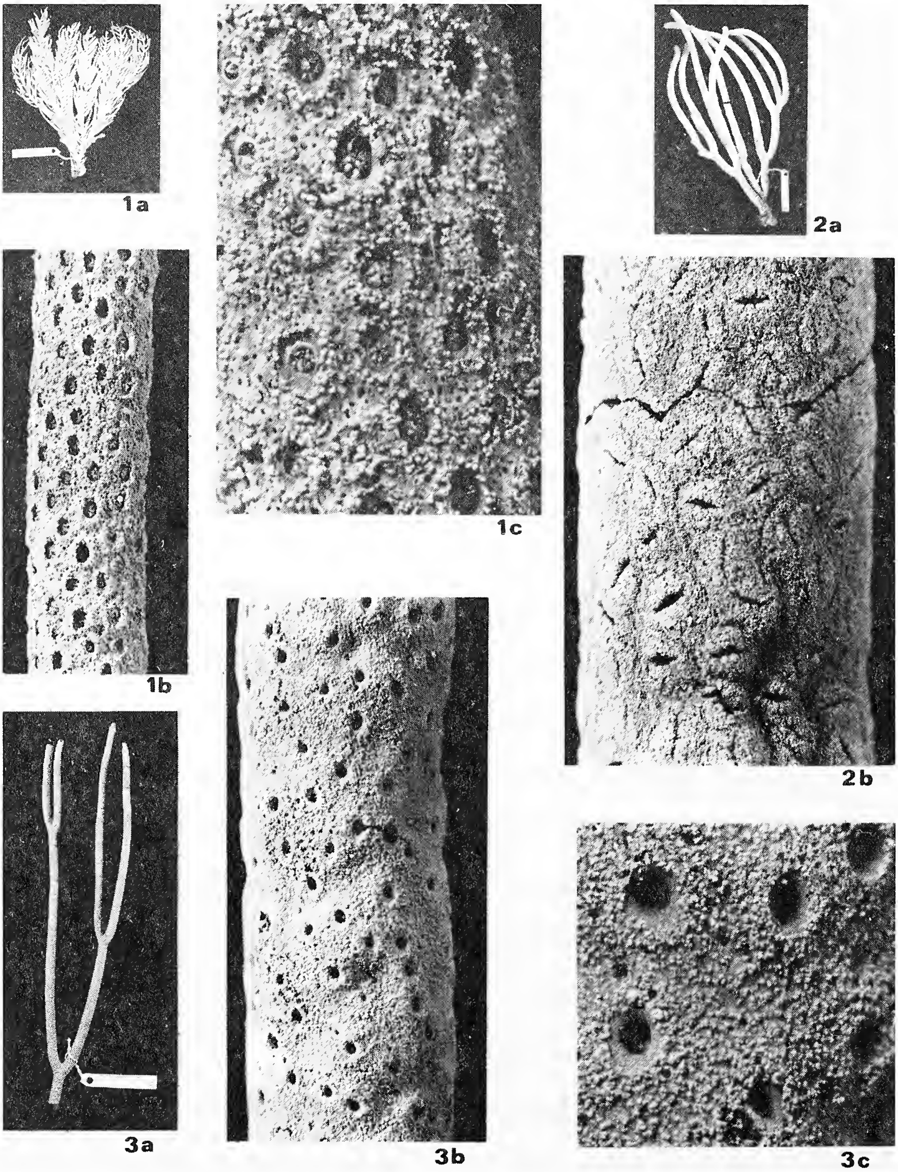

PLATE 5

FIGURE 1. *Muriceopsis flavida*: 1a, label is 75 millimeters in length; 1b, × 6.1; 1c × 18.8.

FIGURE 2. *Plexaurella dichotoma*: 2a, label is 75 millimeters in length; 2b × 3.3.

FIGURE 3. *Plexaurella grisea*: 3a, label is 75 millimeters in length; 3b, × 3.3; 3c × 7.0.

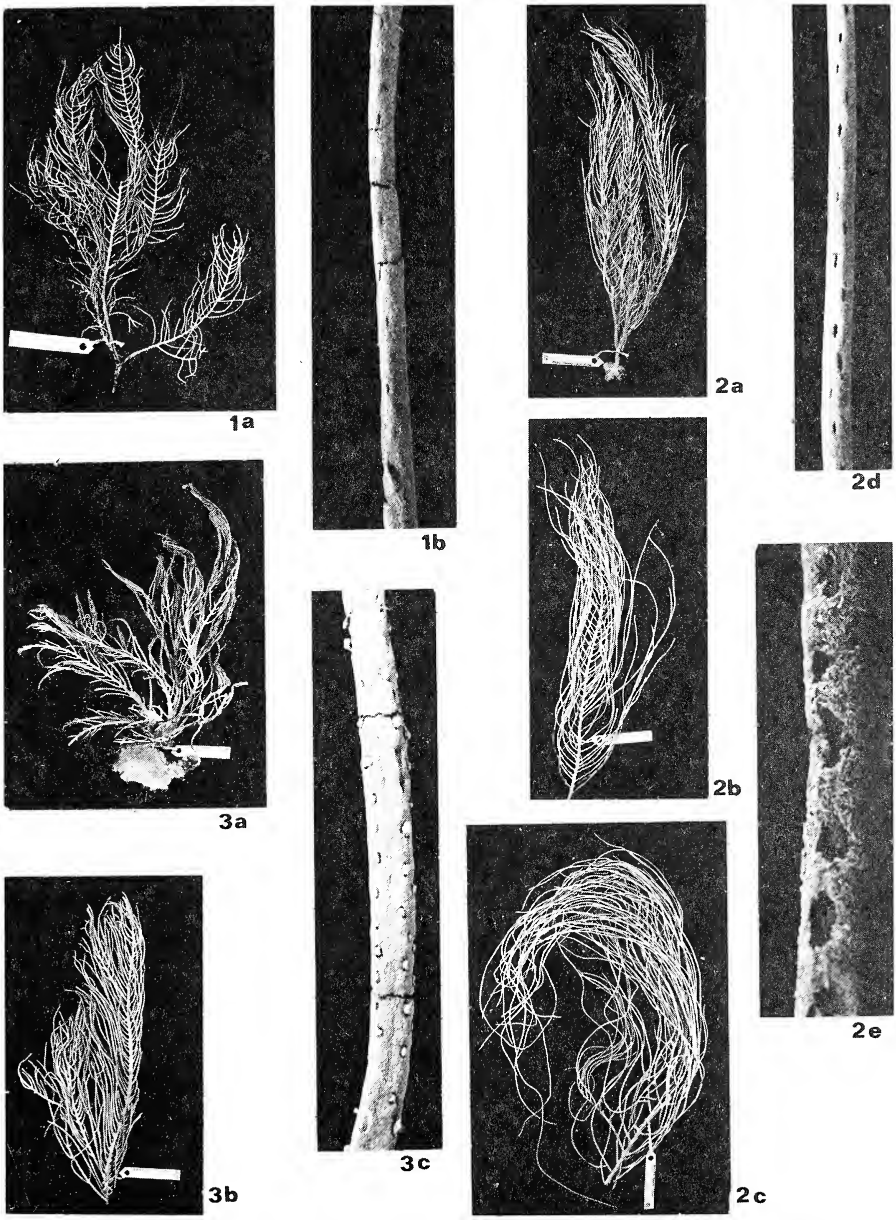

PLATE 6

FIGURE 1. *Pseudopterogorgia bipinnata*: 1a, label is 75 millimeters in length; 1b, × 4.1.

FIGURE 2. *Pseudopterogorgia acerosa*: 2a, 2b, 2c, label is 75 millimeters in length; 2d, × 4.1; 2e, × 9.0.

FIGURE 3. *Pseudopterogorgia americana*: 3a, 3b, label is 75 millimeters in length; 3c, × 3.3.

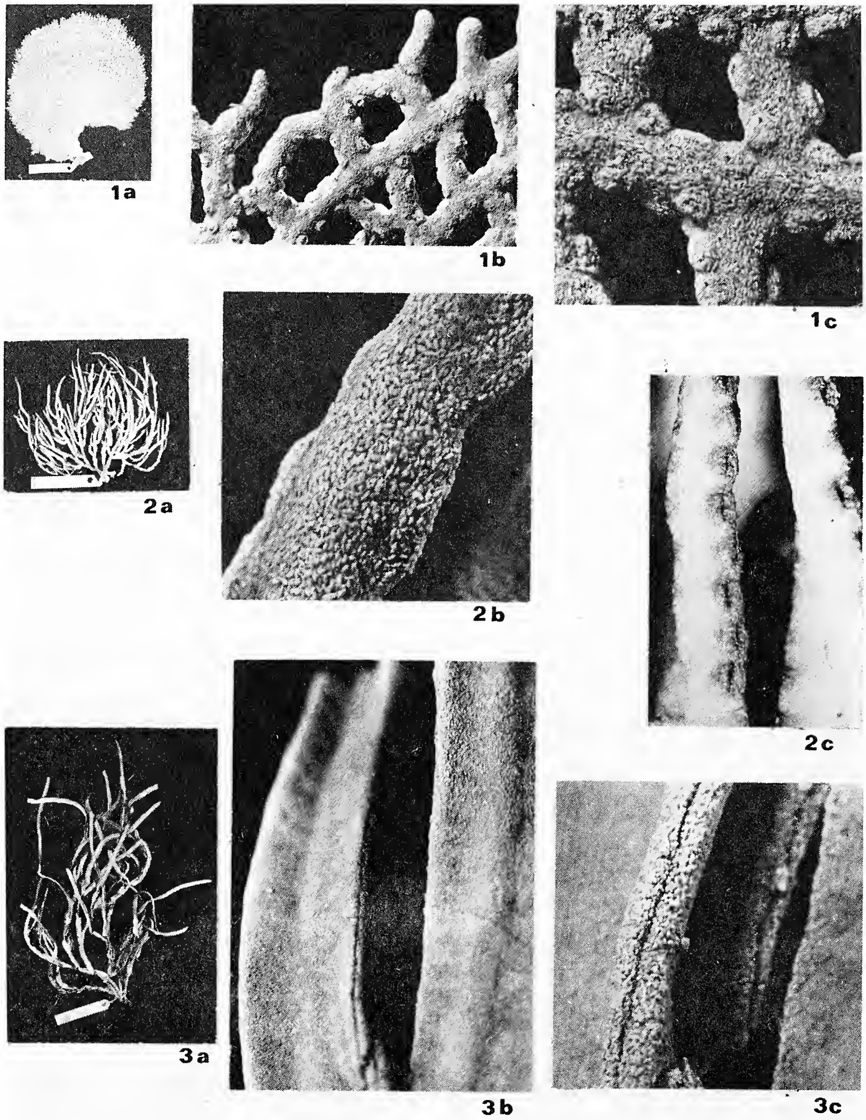

PLATE 7

FIGURE 1. *Gorgonia ventalina*: 1a, label is 75 millimeters in length; 1b, × 4.1; 1c, × 12.3.
FIGURE 2. *Pterogorgia citrina*: 2a, label is 75 millimeters in length; 2b, × 6.5; 2c, × 3.3.
FIGURE 3. *Pterogorgia anceps*: 3a, label is 75 millimeters in length; 3b, × 3.3; 3c, × 7.0.

depth of approximately seven meters. The colony collected was relatively small when compared to other species of the genus and the slender branchlets tend to spread in one plane. The colony dried to a light brown color.

Pseudoplexaura porosa (Houttuyn, 1772)—Plate 3, Figure 1

Specimens were collected from the nearshore environment as well as the leeward side of the island. Water depth ranged from two to 10 centimeters. Most colonies observed were of moderate size (50 centimeters or less. Calcified holdfasts were common.

Pseudoplexaura wagenaari (Stiasny, 1941)—Plate 3, Figure 2

The San Andres species was commonly large (in excess of 50 centimeters in height). Growth environments were the same as for *P. porosa*. The dried colony is ivory white.

Eunicea (Eunicea) mammosa Lamouroux, 1816—Plate 3, Figure 3

Most specimens observed were small (less than 30 centimeters high) and were found on patch reefs in the back-reef lagoon area. In life, colonies were commonly dark brown, becoming light brown or tan when dried.

Eunicea (*Euniceopsis*) *tourneforti* Milne Edwards and Haime, 1857—Plate 4, Figure 2

This species can be found in most environments of the reef complex and the leeward side of the island. The colonies were usually large and robust, measuring up to one meter in height with branches 20 millimeters in diameter. The largest colonies were commonly in deeper water (10 to 20 meters) on the leeward side of San Andres. They usually were attached by calcified holdfasts to submarine cliffs. In life, the colonies were dark blackish brown or gray.

Eunicea sp.—Plate 4, Figure 3

Identification of this specimen is uncertain but according to F. M. Bayer (personal communication, 1978) it is probably in the *tourneforti* complex. Only one specimen was observed in the San Andres area. The colony was attached to a vertical cliff face on the leeward side of the island in approximately 15 meters of water. Light was noticeably dim and it may be that this particular species is more typical of deeper water. The colony was small (less than 20 centimeters in height) with protruding calyces. The lower lip is up-turned. In life, the color was drab gray to blackish brown.

Eunicea (*Euniceopsis*) *calyculata* (Ellis and Solander, 1786)—Plate 4, Figure 1

Eunicea calyculata was rare in the San Andres area and specimens were observed only in the near shore environment in less than three meters of water. The colonies are generally small and light brown in color.

Muriceopsis flavida (Lamarck, 1815)—Plate 5, Figure 1

San Andres species were typically found on the open shelf along the leeward side of the island. Colonies were usually less than 30 centimeters in height and attached by calcified holdfasts. Observed specimens were usually shades of yellow and purple.

Plexaurella dichotoma (Esper, 1791)—Plate 5, Figure 2

Plexaurella dichotoma was relatively common in the San Andres area and typically inhabited the near shore and patch-reef environments and the hard substrate of the leeward side of the island. Colonies usually were stout and attached by calcified holdfasts. Average specimens measured 50 centimeters in height. Color (dried) is light tan to brown.

Plexaurella grisea Kunze, 1916—Plate 5, Figure 3

The habitat of this species was the same as for *P. dichotoma*. The colonies were generally taller and more slender and, when dry, light brown in color.

Family Gorgoniidae Lamouroux, 1812

Pseudopterogorgia bipinnata (Verrill, 1864)—Plate 6, Figure 1

In general *P. bipinnata* was a rare species in the San Andres area. Most colonies noted were not typical growth forms, as they were small and rather fragile. Specimens were found only on the leeward side of the island on open shelf areas. Water depth was approximately six meters.

Pseudopterogorgia acerosa (Pallas, 1766)—Plate 6, Figure 2

Branchlets varied from five centimeters to 30 or 40 centimeters in length. Generally, the smaller specimens were found in the nearshore and patch-reef areas of the main reef complex. On the leeward side of the island, colonies attained heights of nearly two meters with long streaming branchlets. Both in life and dried, the color is light yellow to whitish.

Pseudopterogorgia americana (Gmelin, 1791)—Plate 6, Figure 3

Pseudopterogorgia americana was closely associated with *P. acerosa* in the San Andres area and inhabited the same environments. Both species were attached to hard substrate by noncalcified holdfasts. As noted by

Bayer (1961), *P. americana* may be distinguished by being slimy, in life, caused by the production of large quantities of mucus.

Gorgonia ventalina Linnaeus, 1758—Plate 7, Figure 1

Gorgonia ventalina was probably the most common octocoral in the San Andres area. It was found in almost any environment from fore reef to the deep leeward side of the island. Colonies often were more than one meter in height. Attachment was by a noncalcified holdfast.

Pterogorgia citrina (Esper, 1792)—Plate 7, Figure 2

This species usually was found attached to hard, open substrate on the leeward side of the island. Colonies averaged 15 centimeters high and were attached by a calcified holdfast. Water depth was usually between two and six meters.

Pterogorgia anceps (Pallas, 1766)—Plate 7, Figure 3

Specimens from San Andres were found only on the leeward side of the island in water depths of approximately six meters. They were commonly attached by clacified holdfasts to open shelf areas. The colonies are dark purple (when dried) and average 40 centimeters in height.

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THE RESPONSE OF WOODY VEGETATION TO A TOPOGRAPHIC GRADIENT IN EASTERN TEXAS

E. S. Nixon, J. Matos, and R. S. Hansen
Department of Biology and School of Forestry,
Stephen F. Austin State University,
Nacogdoches, Texas 75962-3003

Abstract.—Changes in woody vegetation in response to a topographic moisture gradient in eastern Texas were determined utilizing the plot method. Sites ranged from creek bottom to upland. The dominant species of trees in the creek bottom, *Ilex opaca*, *Carpinus caroliniana*, *Quercus nigra*, and *Pinus taeda*, decreased in importance along the topographic gradient to upland. *Ostrya virginiana* and *Quercus alba*, principal slope trees, were less important on creek bottom and upland sites. *Pinus echinata*, *Cornus florida*, *Ulmus alata*, and *Quercus stellata* declined in importance from upland to creek bottom, whereas *Liquidambar styraciflua* was an important component of all sites. Species diversity increased from creek bottom to upland. *Key words*: community composition; diversity; topographic gradient.

The occurrence of relatively undisturbed forest communities in eastern Texas is rare. However, when they do occur, these communities provide excellent opportunities to evaluate basic ecological principles. As the remaining relatively undisturbed areas are continually modified by forest management, development, or forest maturation, it becomes increasingly important that data concerning these communities be analyzed and preserved in the literature. This information can serve as a reference point for proper management techniques or as a base line to quantify changes in community structure.

A relatively undisturbed community is associated with Loco Bayou in Nacogdoches County, Texas. Loco Bayou is located about 16 kilometers west of Nacogdoches, Texas; the study area is about three and a half kilometers northwest of the junction of Loco Bayou and Highway 21. The community is associated with a tributary of Loco Bayou. The area has not been logged for more than 30 years.

Three study sites were designated: (1) a creek bottom, (2) a transition or slope site between the creek bottom and upland, and (3) an upland site. The creek was intermittent and contained only pools of stagnant water at the time of study. The creek was generally one to three meters in depth and meandered through a wide bottomland. The bottomland was flat to gently undulating with the creek flowing to the southeast. Evidence indicated that the bottomland was occasionally flooded. Only a small amount of litter was present.

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The east-facing western slope extended from creek bottom to upland. The slope was about 15 to 25 percent and rocks were present. About one to four centimeters of litter covered the soil surface.

The upland was generally flat topographically with a slight overall slope to the southeast. There were two to four centimeters of litter. Although the three study sites are generally mesic, a moisture gradient exists from creek bottom to upland. The creek bottom is more hydric and the upland more xeric than the slope. These conditions allow a study of community composition and species distribution relative to topography. Studies of this kind are lacking and thus needed to better understand the vegetational dynamics of eastern Texas forests.

The study area is located in the Pineywoods Vegetational Area according to Gould (1975). Tharp (1939) classified Nacogdoches County as being a transition zone between the Pine-oak and Longleaf Pine forest types. No single species in the classification of either Gould (1975) or Tharp (1939) is considered dominant, but rather a forest mosaic of many species is common.

Larkin and Bomar (1983) indicated that eastern Texas has a subtropical climate characterized by long summers and mild winters. Average annual precipitation (1951-1980) for Nacogdoches County is approximately 117 centimeters. The average annual temperature for the study area is 18.5° C, with an average annual low of 12.5° C and an average annual high of 25° C. The growing season averages 245 days (Carr, 1967).

Creek bottom soils of the study site are of the Iuka series (thermic Aquic Udifluvents). This soil is a moderately well-drained fine sandy loam, and has a high available water capacity. Runoff is usually slow. The site is subject to brief periods of flooding about once every two to five years (Dolezel, 1980).

Slope and upland soils are of the Cuthbert series (thermic Typic Hapludults). The surface soil is generally a fine sandy loam that is well drained, has moderately slow permeability, and medium available water capacity (Dolezel, 1980). Runoff can be quite rapid on steeper slopes.

METHODS

Woody plant communities of the creek bottom, intermediate slope and adjacent upland were analyzed utilizing the plot method. Individual plots were five by five meters and were arranged in belt transects. Transects were run parallel to the creek in the bottomland areas and parallel with the slope in the slope and upland communities. Forty-six, 50, and 51 plots were analyzed in the creek bottom, slope and upland communities respectively. Trees, shrubs, and woody vines with diameters at breast height (dbh), equal to or greater than half a centimeter, were analyzed. Frequency, density and basal area data were obtained by species. Importance values were determined by summing relative frequency, relative density, and relative basal area.

A one way analysis of variance (ANOVA) was used to determine if communities were significantly different in regard to density and basal area. Upland, slope, and creek bottom communities were also compared with regard to species composition, community similarity, species diversity, evenness, and species richness. Similarity between communities was calculated using Sorensen's index of similarity (Mueller-Dombois and Ellenberg, 1974):

$$IS = (2C/A + B) \times 100,$$

where IS is the index of similarity, C is the number of species common to the two communities being compared, A is the total number of species in community A, and B is the total number of species in community B.

Species diversity was calculated utilizing the Shannon-Weiner Diversity Index:

$$H^1 = -\Sigma \ Pi \log_2 Pi,$$

where Pi is the probability of occurrence of species i (Pielou, 1969).

Species evenness (Pielou, 1969) was determined by:

$$J^1 = H^1/\log S,$$

where H^1 is the Shannon-Weiner Diversity Index and S is the number of species in the sample. Species richness is the number of species in a community. Scientific nomenclature follows Correll and Johnston (1970) except for *Quercus michauxii*, which was not included in the Correll and Johnston manual. Soil samples were collected from the top 15 centimeters of soil in the central area of each community. Soil nutrient content was determined by atomic absorption spectrophotometry and pH by using a Beckman pH meter.

RESULTS

Edaphic

Soil analyses from the three sites, involving calcium, phosphorus, potassium, and magnesium indicated that the slope site appeared to have contained higher levels of these ions and the bottomland the lower levels (Table 1). Low levels of calcium occurred at the creek bottom site whereas phosphorus levels were low at all three sites. Soil pH ranged from 4.3 in the bottom to 6.4 in the upland (Table 1).

Community Diversity

Interestingly, the two dominant tree species of the creek bottom community, *Ilex opaca* and *Carpinus caroliniana*, are representatives of the midstory (Table 2). Principal overstory species are *Quercus nigra*, *Liquidambar styraciflua*, and *Pinus taeda*. The most important shrub species in the creek bottom is *Asimina triloba*, whereas *Vitis rotundifolia* is a common vine. When relating these dominant creek bottom species to the topographic gradient to upland, they decrease in importance (Fig. 1A) with the exception of *L. styraciflua*. *Liquidambar styraciflua* becomes slightly more important in slope and upland communities (Fig. 1D).

TABLE 1. Chemical characteristics of the soils of the study area.

Site location	pH	Exchangeable ions (ppm) Ca	P	K	Mg
Upland	6.4	750	2.0	60	75
Slope	5.2	750	1.0	170	300
Creek-bottom	4.3	150	0.5	75	55

Again, the predominant slope species, *Ostrya virginiana*, is a midstory representative. *Ilex opaca* is also important (Table 2). The overstory is composed primarily of *L. styraciflua*, *Nyssa sylvatica*, *Quercus alba*, and *Q. falcata*. The main component of the shrub layer is *Callicarpa americana*. The most common vine species is *V. rotundifolia*. Topographically, *O. virginiana* and *Q. alba* exhibit their greatest importance in the slope community (Fig. 1B). *Nyssa sylvatica* is slightly more important there than in creek bottom or upland communities (Fig. 1D). *Quercus falcata* is of about the same importance in all three communities (Fig. 1D).

Overstory dominants in the upland community are *Pinus echinata*, *L. styraciflua*, and *Quercus stellata* (Table 2). Associated important midstory species are *Cornus florida* and *Ulmus alata*. *Ilex vomitoria* is the most important shrub, and *V. rotundifolia* and *Smilax laurifolia* are common vines. The importance of dominant upland species, with the exception of *L. styraciflua*, decreases with slope to creek bottom (Fig. 1C).

Variation in elevation from creek bottom to upland results in a topographic moisture gradient. However, community response to this gradient does not necessarily show a continuity with topography. Density, the number of trees, shrubs, and woody vines per hectare, is highest in the upland community (3796 plants), intermediate in the creek bottom community (3409 plants) and lowest in the slope community (3088 plants). Even though differences exist, there were no significant differences ($P = 0.05$) in density in regard to the three communities. Community basal area responds somewhat differently than density with the creek bottom community having 44.4 square meters per hectare, the upland community 39.4, and the slope 33.4. There were also no significant differences in basal area between the three communities. Species richness ranged from 31 species in the creek bottom community to 35 species in the slope community. The upland community had 34 species.

Sorenson's Index of Similarity (IS) indicates that the creek bottom and slope communities most closely resemble each other (IS = 70) (Fig. 2). Slope and upland communities are also similar (IS = 64), whereas upland and creek bottom communities had the least similarity (IS = 55). Thus, community diversity is not great along the topographic moisture gradient.

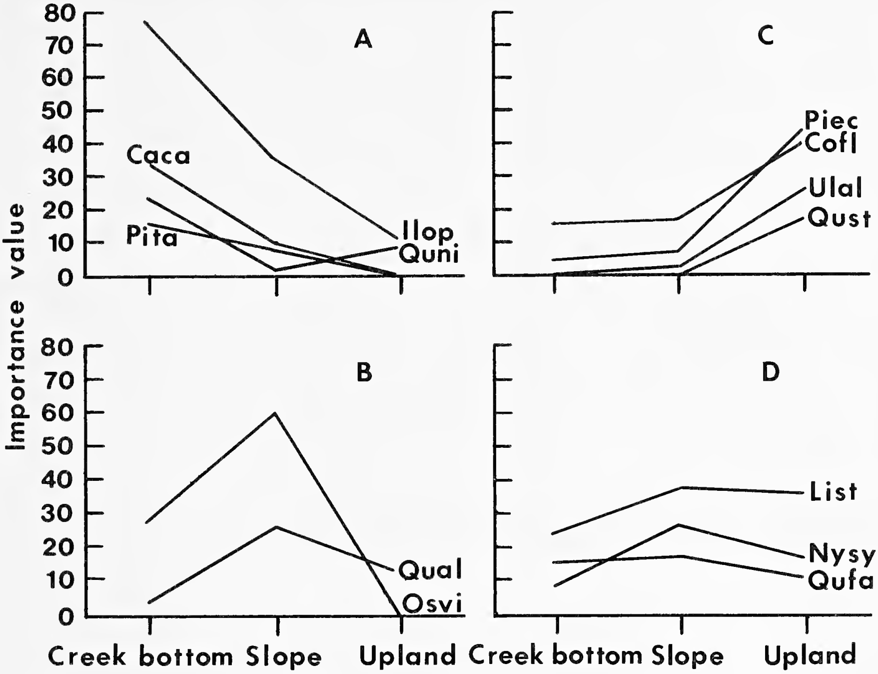

FIGURE 1. Species distribution along a topographic gradient: A—Important creek bottom species (Ilop = *Ilex opaca*, Quni = *Quercus nigra*, Caca = *Carpinus caroliniana*, Pita = *Pinus taeda*); B—Important slope species (Qual = *Quercus alba*, Osvi = *Ostrya virginiana*); C—Important upland species (Piec = *Pinus echinata*, Cofl = *Cornus florida*, Ulal = *Ulmus alata*, Qust = *Quercus stellata*); D—Important species in all three communities (List = *Liquidambar styraciflua*, Nysy = *Nyssa sylvatica*, Qufa = *Quercus falcata*).

Species evenness varied from .657 in the creek bottom community to .727 in the slope community and .810 in the upland community. Species diversity also reflected a consecutiveness associated with the topographic moisture gradient. The species diversity index was 3.252 in the creek bottom, 3.727 on the slope, and 4.119 in the upland.

DISCUSSION

Woody creekside vegetation in eastern Texas has received little attention, but concern and interest in these communities has increased in recent years. Tharp (1939), in his work in the pine-oak forests of eastern Texas, listed American hornbeam (*Carpinus caroliniana*), eastern hophornbeam (*Ostrya virginiana*), water elm (*Planera aquatica*), and mulberry (*Morus rubra*) as common species along creeks. In the current study, *M. rubra* was of minor importance and *P. aquatica* was absent. However, *C. caroliniana* and *O. virginiana* were important components along with *Quercus nigra*, *N. sylvatica*, *L. styraciflua*, *P. taeda*, *Q.*

TABLE 2. Density, basal area, and importance value data for dominant species of creek bottom, slope, and upland communities.

	Creek bottom community			Slope community			Upland community		
Species	Density stems/ha	Basal area m^2/ha	IV[1]	Density stems/ha	Basal area m^2/ha	IV	Density stems/ha	Basal area m^2/ha	IV
Ilex opaca	1339	7.166	76.23	528	1.236	34.97	148	1.272	11.26
Liquidambar styraciflua	191	3.787	22.64	336	4.629	36.87	432	4.357	34.75
Ostrya virginiana	384	2.340	26.99	824	5.228	58.92	8	.001	.55
Cornus florida	228	.360	16.44	232	.462	17.40	784	2.377	40.39
Pinus echinata	8	2.066	5.41	32	2.019	8.39	260	11.978	42.01
Carpinus caroliniana	452	2.930	32.87	136	.546	9.27	—	—	—
Quercus falcata	44	4.923	14.36	94	3.878	18.35	88	2.594	11.59
Nyssa sylvatica	36	2.917	9.59	200	3.790	25.10	96	.754	8.16
Quercus alba	36	.301	3.70	80	6.210	24.81	88	2.682	12.16
Quercus nigra	52	8.290	23.20	16	.362	2.41	72	2.264	10.00
Ulmus alata	—	—	—	16	.036	1.44	400	1.310	24.82
Quercus stellata	—	—	—	—	—	—	64	5.140	17.43
Pinus taeda	716	7.708	22.15	312	2.566	9.66	—	—	—

[1] Importance value is equal to the sum of relative frequency, relative density and relative basal area. Other species listed in order of importance: Creek bottom—*Vitis rotundifolia* (9.22), *Sassafras albidum* (6.48), *Acer rubrum* (5.62), *Vitis* sp. (3.37), *Smilax rotundifolia* (3.29), *Tilia* sp. (3.14), *Asimina triloba* (2.47), *Quercus phellos* (1.80), *Carya aquatica* (1.51), *Acer saccharum* (1.51), *Morus rubra* (1.02), *Vaccinium arboreum* (0.77), *Callicarpa americana* (0.76), *Smilax bona-nox* (0.76), *Gelsemium sempervirens* (0.76), *Carya cordiformis* (0.76), *Smilax laurifolia* (0.76), *Parthenocissus quinquefolia* (0.76), *Ilex montana* (0.76), *Juniperus virginiana* (0.76): Slope—*Morus rubra* (9.60) *Acer rubrum* (6.80), *Acer saccharum* (4.53), *Carya texana* (4.12), *Sassafras albidum* (3.38), *Callicarpa americana* (2.26), *Vitis rotundifolia* (2.06), *Fraxinus pennsylvanica* (2.00), *Ulmus rubra* (1.66), *Prunus serotina* (1.65), *Aralia spinosa* (1.64), *Carya cordiformis* (1.35), *Tilia* sp. (1.35), *Viburnum rufidulum* (1.35), *Chionanthus virginica* (1.34), *Fraxinus americana* (1.34), *Carya aquatica* (1.33), *Vaccinium arboreum* (1.33), *Rhus copallina* (0.73), *Melia azedarach* (0.67), *Berchemia scandens* (0.66), *Vitis* sp. (0.66), *Smilax bona-nox* (0.66): Upland—*Vitis rotundifolia* (11.35), *Carya texana* (10.35), *Smilax laurifolia* (9.96), *Viburnum rufidulum* (8.71), *Ilex vomitoria* (7.78), *Prunus serotina* (7.23) *Acer rubrum* (4.44), *Euonymus americanus* (4.13), *Smilax rotundifolia* (3.38), *Rhus toxicodendron* (3.36), *Juniperus virginiana* (2.61), *Vitis* sp. (2.24), *Vaccinium arboreum* (2.19), *Ulmus rubra* (1.92), *Carya cordiformis* (1.50), *Berchemia scandens* (1.09), *Carya tomentosa* (0.78), *Ilex decidua* (0.77), *Quercus velutina* (0.75), *Prunus mexicana* (0.59), *Morus rubra* (0.58), *Celtis laevigata* (0.56), *Fraxinus pennsylvanica* (0.56).

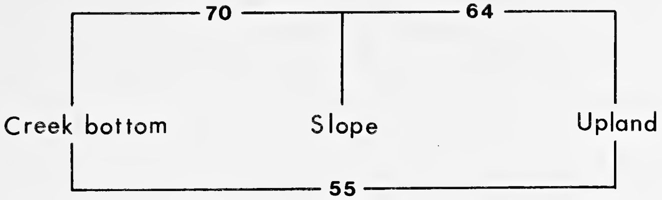

FIGURE 2. Sorenson's Similarity Indices for creek bottom, slope, and upland communities.

falcata, and *I. opaca*. Our results are more comparable to the mesic creek bottoms in recent studies by Sullivan and Nixon (1971) and Nixon and Raines (1976), where *C. caroliniana*, *L. styraciflua*, *Q. nigra*, and *O. virginiana* were dominant. The only major difference was the dominance of *I. opaca* in our study. Other mesic creek bottom communities analyzed in eastern Texas indicate the importance of *Fagus grandifolia*, *Magnolia grandiflora*, *P. taeda*, *Quercus michauxii*, *Fraxinus americana*, *Acer saccharum*, *Tilia* sp., and *Halesia diptera* (Wilkinson, 1982; Nixon et al., 1983).

In Alabama, Gemborys and Hodgkins (1971) and Golden (1979) listed *F. grandifolia*, *Liriodendron tulipifera*, *Q. nigra*, *C. caroliniana*, *Acer rubrum*, *L. styraciflua*, *N. sylvatica*, *C. florida*, *Pinus elliottii*, *Q. falcata*, *Symplocos tinctoria*, and *I. opaca* as important inhabitants of small mesic stream bottoms. Except for *L. tulipifera* and *P. elliottii*, which are not native to eastern Texas, these taxa are notable creek-bottom components in eastern Texas. Disregarding *F. grandifolia* and *S. tinctoria*, all of the above-mentioned species are prominent at Loco Bayou. Sixty-eight percent of the small stream bottom taxa listed by Golden (1979) are in common with those at Loco Bayou.

Based on importance values, the slope community we studied consisted chiefly of *O. virginiana*, *L. styraciflua*, *I. opaca*, *N. sylvatica*, *Q. alba*, *Q. falcata*, and *C. florida*. Mesic slope forests in the Big Thicket of southeastern Texas contain *Q. falcata*, *Q. alba*, *P. taeda*, *P. echinata*, *M. grandiflora*, and *F. grandifolia* as principal overstory species (Marks and Harcombe, 1981).

Although dominant canopy species vary from those at Loco Bayou, mesic slope communities in eastern Tennessee have 63 percent of their species in common with the Loco Bayou slope community (Skeen, 1973). *Quercus alba* is the dominant species on lower slopes in the lower Alabama Piedmont (Golden, 1979).

In the upland community of our study, *P. echinata*, *C. florida*, *L. styraciflua*, *U. alata*, and *Q. stellata* were important species. In a study of upland communities, Sullivan and Nixon (1971) found *Carya* sp., *Q. falcata*, and *Sassafras albidum* to have high importance values in addition to those found in our study, but did not include *U. alata*. Langston (1974) analyzed three relatively undisturbed mesic upland sites in Nacogdoches and Rusk counties of eastern Texas. She found *P. taeda*, *C. florida*, *Q. falcata*, *U. alata*, *L. styraciflua*, *P. echinata*, *Q. alba*, and *N. sylvatica* to have the highest importance values. Her results compare favorably with the results of our study for both the slope and the upland communities. In southeastern Texas (Chambers County), *P. taeda*, *L. styraciflua*, *Q. phellos*, *Q. nigra*, *Q. falcata*, *M. grandiflora*, and hickories were important mesic upland components (Harcombe and Neaville, 1977). *Ilex vomitoria* and *C. americana* were predominant shrubs. Mesic uplands in the lower Alabama Piedmont contained *Q. alba*, *Q. falcata*, *Q. stellata*, *C. florida*, *Carya tomentosa*, *N. sylvatica*, *P. taeda*, and *P. echinata* as prominent species, thus showing a high similarity to the eastern Texas community.

It has been suggested that species diversity increases as a particular stress diminishes (Barbour et al., 1980). Although this may vary with circumstance, it appears to hold true in our study. The creek bottom, which contains a more stressful environment because of periodic flooding, has the lowest species diversity ($H^1 = 3.25$). The index was 3.73 in the slope community and 4.12 in the mesic upland community. Bell (1977) noted that species richness and diversity increased with decreased flood stress.

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GENERAL NOTES

PHAENICIA (DIPTERA: CALLIPHORIDAE) MYIASIS IN A THREE-TOED BOX TURTLE, *TERRAPENE CAROLINA TRIUNGUIS* (REPTILIA: EMYDIDAE), FROM ARKANSAS

CHRIS T. MCALLISTER
Renal-Metabolic Laboratory (151-G), Veterans Administration Medical Center,
4500 S. Lancaster Road, Dallas, Texas 75216, and Department of Biological
Sciences, North Texas State University, Denton, Texas 76203

Instances of sarcophagid myiasis have been reported in ornate box turtles (*Terrapene ornata ornata*) from Kansas (Rainey, 1953; Legler, 1960) and Oklahoma (McMullen, 1940; Rodeck, 1949), in eastern box turtles (*Terrapene carolina carolina*) from Illinois (Peters, 1948; Rokosky, 1948) and Florida (King and Griffo, 1959), and in a three-toed box turtle (*T. c. triunguis*) from Mississippi (Jackson et al., 1969). To my knowledge, larval dipterans of the family Calliphoridae have not been reported previously to cause myiasis in turtles of the genus *Terrapene*. Here I report a case of wound myiasis by a calliphorid fly in *T. c. triunguis* from central Arkansas.

The host, an adult female (carapace length, 12.0 centimeters) was captured on 11 October 1986, 3.2 km. SW Shannon Hills, Saline Co., Arkansas. Upon close inspection, the turtle was found to be suffering from a foul-smelling and supporting lesion along the anterior plastron bridge separating the humeral and pectoral scutes. Protruding from the festered wound were four larval calliphorid maggots of the genus *Phaenicia*. After extracting the larvae, the necrotic tissue was cleansed with 70 percent isopropanol and the turtle was released.

Specific identification of *Phaenicia* depends upon characters found in other life stages and precise determination is possible only by rearing flies to adulthood. Interestingly, maggots of the green bottle fly (*P. sericata*) occur primarily on carrion and secondarily in feces, garbage, and various other substances, and occasionally plant matter (Greenberg, 1984). The literature contains numerous accounts of case histories and general accounts of calliphorid infestation in animals (see Hall, 1948). In addition, *P. sericata* has been reported to produce wound myiasis in humans (James, 1947; Greenberg, 1984; and others).

In the present case, it appears that the myiasis was confined to the necrotic tissue (that is, benign infection). However, under certain circumstances *Phaenicia* may be a serious parasite that can burrow below superficial necrotic tissue (James, 1947; Stewart and Foote, 1974).

I thank N. E. Woodley (Systematic Entomology Laboratory, USDA, Beltsville, Maryland) for identifying the larvae and W. Stuart for technical assistance.

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CLAPPER RAIL (*RALLUS LONGIROSTRIS*) IN WEST-CENTRAL TEXAS

D. Brent Burt, Donna Burt, Terry C. Maxwell, and Delbert G. Tarter
Department of Biology, Angelo State University, San Angelo, Texas 76909, and 2903 Chatterton Dr., San Angelo, Texas 76904 (DGT)

On 20 August 1986, a clapper rail (*Rallus longirostris*) was captured in a small marsh above the south shore of Lake Nasworthy, San Angelo, Tom Green Co., Texas. The bird was flushed from a small mixed patch of cattail (*Typha* sp.) and bulrush (*Scirpus* sp.) at the margin of a mud flat; plumage characters indicated it was a young of the year of unknown sex. The rail was photographed, banded with a U.S. Fish and Wildlife Service band (no. 715-47556), and released. The identification was confirmed from the photographs, which were examined by Richard C. Banks and Storrs L. Olson at the National Museum of Natural History, Washington, D.C. Copies of the photographs are deposited in the Texas Photo-Record File (entry no. 402), at Texas A&M University.

This is the first reported occurrence of the clapper rail inland from the coastal plain of Texas. The locality is approximately 450 kilometers from the nearest salt and brackish marsh-inhabiting populations found in Hidalgo and Wharton counties (Oberholser, 1974; Arnold, 1984). In the eastern United States, clapper rails are known to be confined as breeders to salt marshes. The closely related king rail (*R. elegans*), which is similar in appearance, inhabits freshwater marshes, and has been reported regularly as a migrant and sporadically as a breeder throughout much of Texas (Oberholser, 1974; Arnold, 1984). This habitat distinction has been regarded as an important isolating mechanism between the two species (Ripley, 1977), and has resulted in the general belief that inland-occurring, large, long-billed *Rallus* invariably are king rails. The species are difficult to distinguish in the field, but this record confirms that clapper rails can be found inland from salt marshes.

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DISTRIBUTIONAL RECORDS FOR SIX TEXAS MAMMALS

Brian R. Chapman and Sandra G. Spencer
Department of Biology, Corpus Christi State University,
Corpus Christi, Texas 78412

Examination of the vertebrate collection at Corpus Christi State University has brought to light several noteworthy distributional records of mammals from Texas. In addition to information on known ranges, pertinent ecological notes are included for certain of the species.

Lasionycteris noctivagans (Le Conte).—Although reported from a wide area of North America (Hall, 1981) and from several Trans-Pecos counties (Blair, 1952; Judd and Schmidly, 1969; Schmidly, 1977), the silver-haired bat is rare in Texas. On the evenings of 17 and 18 April, 1987 we captured five specimens (CCSU 1180-1184) in mist nets set above a small pool in ZH Canyon on the Clay E. Miller Ranch, 14.5 km. SW Valentine, Presidio County, Texas. The canyon contained scattered oaks (*Quercus* sp.) and the pool was surrounded on two sides by cottonwood trees (*Populus* sp.). Three males and two females were captured within an hour after sunset; of the two females taken on subsequent evenings, each was in the company of a male. These specimens represent the first taken from Presidio County and the southernmost records from Texas.

Thomomys bottae limitaris (Goldman).—Botta's pocket gopher is known from a wide variety of ecological conditions throughout the Trans-Pecos region of Texas. However, Schmidly (1977) showed no record of the species in Pecos County. The capture of a female Botta's pocket gopher (CCSU 613) in the Glass Mountains, 40.5 km. N Marathon, on 15 October 1978 extends the known range at least 40 kilometers northward and establishes the presence of the species in Pecos County. The specimen was captured in an alligator juniper (*Juniperus deppeana*)—Mexican pinyon (*Pinus cembroides*) association on rocky soil. We follow Hoffmeister (1969) in referring the species to *T. bottae*.

Dipodomys ordii medius (Setzer).—A male Ord's kangaroo rat (CCSU 185) with enlarged testes was captured on 28 September 1976 in a catclaw (*Mimosa* sp.)-creosote bush (*Larrea tridentata*) association 9 km. N Iraan, Crockett County, Texas. Although *D. ordii* occurs throughout much of the Trans-Pecos in areas with loose, sandy soil, it has not been reported previously from Crockett County. This record also extends the range of the species eastward across the Pecos River in southwestern Texas. The specimen was taken in a disturbed habitat with scattered dunelets of windblown sand.

Reithrodontomys montanus montanus (Baird).—A single specimen (male, CCSU 630) was taken in a creosote bush-mixed species grassland 51 km. E El Paso, El Paso County, on 20 April 1980. Although it has been previously reported from El Paso County (Schmidly, 1977), its occurrence in the area and the paucity of ecological data warrant an additional report. The specimen, which showed no evidence of reproductive activity, was captured in the flat, grassy plain approximately eight kilometers south of the entrance to Hueco Tanks State Park. A total of 15 specimens was captured in the area, but all except the one reported herein were released.

Neotoma micropus canescens (J. A. Allen).—The southern plains woodrat occupies desert scrub habitats at lower elevations throughout the Trans-Pecos (Schmidly, 1977). A male *N. micropus* was trapped in a prickly pear (*Opuntia* sp.) clump approximately 19 km. N Iraan, Crockett County, on 27 September 1976. This locality represents the easternmost record of the species in that portion of the state and extends the known range across the Pecos River about 20 kilometers.

Urocyon cinereoargenteus scottii (Mearns).—According to Davis (1974), gray foxes occur throughout the state south of the Panhandle region. However, there are few records of the species in southern Texas and only one record (Halloran, 1961) from a Texas coastal area.

This account establishes the presence of the species in three coastal counties of south-central Texas. A male (CCSU 515) was found dead on a road (DOR) 1 km. S Copano Bay on highway 35, Aransas County, on 31 January 1977. A male (CCSU 516) was killed by landowners within the Corpus Christi City limits, Nueces County, on 24 February 1978. A female (CCSU 517) was found DOR at the port Lavaca City Limits, Calhoun County, on 1 January 1980. In addition, at least three gray foxes inhabit the Ward Island campus of Corpus Christi State University, Nueces County.

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DISTRIBUTIONAL NOTES ON FOUR SPECIES OF TEXAS MAMMALS

Jim R. Goetze and Larry L. Choate
Department of Biology, Midwestern State University,
Wichita Falls, Texas 76308

Specimens of four species from the Collection of Recent Mammals at Midwestern State University (MWSU) contribute to our knowledge of the distributional status of these taxa in Texas.

Spermophilus mexicanus.—The Mexican ground squirrel has been documented as occurring westward in Texas at least as far as the eastern flatlands of the Trans-Pecos region (Schmidly, 1977), although Dalquest and Stangl (1986) listed the species as a hypothetical resident of the adjacent Apache Mountains of Culberson County. An adult male (MWSU 14544, scrotal testes measuring 17 by 9 mm) was obtained on 9 March 1987 at the base of a *Dipodomys spectabilis* mound, situated on the lower flank of the Apache Mountains, 6 mi. NNW Kent, Culberson County. This record of *S. mexicanus* in Texas extends the range of the species somewhat westward and into the higher elevations of the Front Range, where it probably is limited to lower slopes and alluvial fans. Whether the squirrel was using the kangaroo rat den or foraging nearby could not be determined.

Dipodomys spectabilis.—The banner-tailed kangaroo rat mostly is restricted to the Trans-Pecos region in Texas, although Archer (1975) listed a northernmost record for the state in Gaines County. Five specimens from 6 mi. W Patricia, Dawson County, represent the first records from that county and a slight northeastern extension of the known range this species. None of four females, collected on 14 April 1968 (MWSU 6035, 6084) and on 2 April 1969 (MWSU 7318, 8425), was pregnant. Site of the collection was a grassy pasture with scattered mesquite, next to a grain field.

Mephitis mephitis.—The striped skunk occurs throughout Texas. However, records from the northern part of the Trans-Pecos are sparse (Schmidly, 1977, 1984). In Culberson County, the species is known only from the Guadalupe Mountains. The weathered skull of a striped skunk (MWSU 14485) was found next to a small metal stock tank, 6 mi. N Kent, at the base of the Apache Mountains. *Mephitis mephitis* was listed by Dalquest and Stangl (1986) as a hypothetical resident of these desert foothills.

Canis lupus.—The subfossil lower canine of a gray wolf (MWSU 14198) was found along a sandy stream bank on Beaver Creek, 9.5 mi. SSE Oklaunion, Wilbarger County. Post-Pleistocene or Recent records of *C. lupus* from Texas are scarce, and the only previous record from north-central Texas is of a jaw fragment from Montague County, nearly 100 miles to the east of the present site (Dalquest and Horner, 1984). An early-Recent (and probably pre-Columbian) fauna consisting, in part, of *Canis latrans*, *Lepus californicus*, *Bison bison*, and *Sylvilagus* sp. was associated with the tooth.

We wish to thank F. B. Stangl, Jr., and W. W. Dalquest for their reviews of this manuscript.

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ROBERT R. HOLLANDER AND RICHARD W. MANNING
The Museum and Department of Biological Sciences,
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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 were 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 by authors in titles or as key words.

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