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The Texas Journal of Science is published quarterly in February, May, August, and November for $30 per year (regular membership) by The Texas Academy of Science. Second-class postage rates (ISSN 0040-4403) paid at Lubbock, Texas. Postmaster: Send address changes, and returned copies to The Texas Journal of Science, Box 43151, Texas Tech University, Lubbock, Texas 79409-3151, U.S.A.
NOTEWORTHY RECORDS OF MAMMALS FROM THE EDWARDS PLATEAU OF CENTRAL TEXAS

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Abstract.—Distributional notes based upon recent field collections are reported for nine species of small mammals from the Edwards Plateau of central Texas. These include one species of bat (Nycticeius), one armadillo (Dasypus), one kangaroo rat (Dipodomys), four mice (Reithrodontomys, Peromyscus and Baiomys), one woodrat (Neotoma) and one skunk (Conepatus).

Field studies conducted from 1990 through 1993 have provided additional distributional data on several species of small mammals from the Edwards Plateau of central Texas. Additional noteworthy specimens from this same geographical area were also noted to be present in the Collection of Recent Mammals of The Museum, Texas Tech University. The following species accounts are the result of research efforts conducted during the course of this study. Voucher specimens are deposited with the holdings of The Museum at Texas Tech University (TTU).

Nycticeius humeralis humeralis (Rafinesque)
(Evening Bat)

Distributional notes.—The evening bat is found throughout the eastern half of Texas and reaches its western distributional limits on the Edwards Plateau (Schmidly 1991). While specimens are reported from several counties on the Edwards Plateau (Manning et al. 1987; Schmidly 1991; Dowler et al. 1992), overall representation from this geographical area of Texas is poorly known. This report represents, the first specimen record of the evening bat from Blanco County.

Material examined.—1 mi N, 10 mi E of Johnson City, Blanco County, Texas, 13 May 1990, three specimens (TTU 57802-57804) netted over small stream. A single specimen (TTU 57804) was gravid with two fetuses measuring 20 mm in crown-rump length.
Dasypus novemcinctus mexicanus Peters
(Nine-banded Armadillo)

Distributional notes.—Although the armadillo has been reported to range throughout eastern and southern Texas (Schmidly 1983) and is currently expanding its range onto the Llano Estacado (Jones et al. 1993), records of its occurrence from the northern Edwards Plateau are rare. The recent collection of a single specimen from near Buffalo Gap represents the first specimen record of this species from Taylor County.

Material examined.—2 mi S, 8 mi W of Buffalo Gap, Taylor County, Texas, 27 June 1993, one specimen (TTU 63410).

Habitat.—The collection locality is in rough, broken lands of the Callahan Divide, which is a northern extension of the Edwards Plateau.

Dipodomys merriami ambiguus Merriam
(Merriam’s Kangaroo Rat)

Distributional notes.—While Merriam’s kangaroo rat has been reported from several Texas counties east of the Pecos River (Jones & Jones 1992), the distribution of this species is poorly known for this region. It has been reported from adjacent Midland, Reagan (Jones & Jones 1992), and Crockett Counties (Hollander et al. 1987). This report represents the first record of this species from Upton County.

Material examined.—5 mi S, 4 mi E of Crane, Upton County, Texas, 19 March 1992, three specimens (TTU 63074-63076).

Habitat.—The collection locality is adjacent to a fencerow which borders a mesquite pasture. Vegetation in this area consisted of mesquite (Prosopis glandulosa), creosote (Larrea tridentata), grama grass (Bouteloua sp.) and broomweed (Guitierrezia sp.). Soils at the locality were eroded from a nearby escarpment and were sandy with small gravel.

Reithrodontomys fulvescens laceyi Allen
(Fulvous Harvest Mouse)

Distributional notes.—Schmidly (1983) reported this species from Bosque and Hays Counties of central Texas. This report represents additional county records for the Callahan Divide and Edwards Plateau.
Material examined.—8 mi S, 4.5 mi W of Clyde, Callahan County, Texas, 15 July 1991, one specimen (TTU 59852). 4.5 mi N of Oplin, Callahan County, Texas, 6 June 1993, one specimen (TTU 63418). 3.5 mi E of San Saba, San Saba County, Texas, 16 July 1992, one specimen (TTU 63419).

Reithrodontomys megalotis megalotis (Baird)
(Western Harvest Mouse)

Distributional notes.—The western harvest mouse ranges from the Llano Estacado south into the Trans-Pecos area of west Texas. This species was previously believed to be restricted to the Llano Estacado at the extreme southeastern part of its range (Davis 1974). This is the first report of the western harvest mouse from Glasscock County. Choate et al. (1992) mentioned the possible occurrence of this species in this county at the southern border of the Kansan Biotic Province. The collection locality is, however, on the Edwards Plateau immediately east of the Llano Estacado.

Material examined.—8.5 mi N, 7 mi W of Garden City, Glasscock County, Texas, 1 April 1990, five specimens (TTU 59103-59107).

Peromyscus attwateri (Allen)
(Texas Mouse)

Distributional notes.—The Texas mouse is distributed from central Texas north to the Red River and west to the escarpment of the Llano Estacado (Davis 1974). This report represents a new county record for this species within its known range. The collection site is within the Callahan Divide.

Material examined.—1 mi S, 9 mi W of Buffalo Gap, Taylor County, Texas, 27 June 1993, one specimen (TTU 63425).

Habitat.—The collection locality was a rocky slope dominated by juniper (Juniperus ashei) and sideoats grama (Bouteloua curtipendula).

Baiomys taylori taylori (Thomas)
(Pygmy Mouse)

Distributional notes.—The geographic range of the pygmy mouse in Texas has been well documented (Davis 1974; Jones et al. 1987; Choate et al. 1990; Jones et al. 1993). This species is distributed over the eastern two-thirds of the state and onto the Llano Estacado and adjacent
areas. Several specimens collected during the course of this study represent county records from within its range.

**Material examined.**—2 mi W of Oplin, 15 July 1991, five specimens (TTU 59834-59838); 1.5 mi N of Oplin, 6 June 1993, one specimen (TTU 63442); 4.5 mi N of Oplin, Callahan County, Texas, 6 June 1993, one specimen (TTU 63443). 4 mi W of Big Lake, Reagan County, Texas, 22 July 1991, two specimens (TTU 59841-59842). 3.5 mi E of San Saba, San Saba County, Texas, 16 July 1992, two specimens (TTU 63447-63448). 5 mi S, 4 mi E of Crane, Upton County, Texas, 19 March 1993, one specimen (TTU 63077). 4 mi S, 5 mi W of Eden, Concho County, Texas, 19 June 1993, one specimen (TTU 63444). 1 mi N, 4 mi W of San Marcos, Hays County, Texas, 16 July 1993, two specimens (TTU 63445-63446).

**Habitat.**—All specimens were collected from habitats characterized by dense vegetative cover.

*Neotoma micropus micropus* Baird
(Southern Plains Woodrat)

**Distributional notes.**—The southern plains woodrat ranges throughout the western two-thirds of Texas (Jones & Jones 1992). This record represents the first reported occurrence of this species from Callahan County. The collection locality lies within the Callahan Divide of the Edwards Plateau. The species has been reported from adjacent Eastland and Taylor Counties.

**Material examined.**—8 mi S, 4.5 mi W of Clyde, Callahan County, Texas, 15 July 1991, one specimen (TTU 59844).

**Habitat.**—The specimen was collected from a rocky slope dominated by juniper and grama grasses.

*Conepatus mesoleucus mearnsi* Merriam
(Hog-nosed Skunk)

**Distributional notes.**—The currently known range of the hog-nosed skunk in Texas was reported by Manning et al. (1986). While this report noted a sight record of *C. mesoleucus mearnsi* from Nolan County, no voucher specimens were collected. This current study reports the first voucher of the hog-nosed skunk from Nolan County as well as the first specimen record of this species from Reagan County on the western Edwards Plateau.
Material examined.—1 mi S of Big Lake, Reagan County, Texas, 1 September 1991, one specimen (TTU 60063). 6 mi N, 7 mi E of Blackwell, Nolan County, 17 August 1993, one female specimen (TTU 63450), partial salvaged skull, no reproductive activity noted, external measurements: total length, 660 mm; tail length, 257 mm; hind foot, 70 mm; length of ear from notch, 28 mm.

Acknowledgments

We are grateful to Richard W. Manning and an anonymous reviewer for their critical reviews of this manuscript.

Literature Cited


A FOSSIL SPECIMEN OF THE LONG-NOSED SNAKE
RHINOCHEILUS FROM THE PLIOCENE OF
SOUTHERN NEW MEXICO

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Abstract.—This study reports a Blancan (late Pliocene) fossil snake from southern New Mexico. This is the first documentation of a late Cenozoic fossil snake from New Mexico and the first state fossil record of the genus *Rhinocheilus*. It also extends the western range of the known fossil distribution of *Rhinocheilus* and appears to represent the currently known most complete fossil specimen of the long-nosed snake.

The Miocene-Pleistocene Santa Fe Group, which is the sedimentary fill of the Rio Grande rift basins of central New Mexico, is known to contain extensive assemblages of fossil mammals (Tedford 1981). Much less collected and studied are the fossil herpetofaunas of these strata (Kues 1993). The fossil specimen detailed in this study was collected at the New Mexico Museum of Natural History and Science (NMMNH) locality 02834 in the NE1/4 NE1/4 SW1/4 NW 1/4 sec. 23, T19S, R4W, Doña Ana County, New Mexico. This stratum is in the lower part of the Camp Rice Formation of the Santa Fe Group. Fossil mammals associated with this stratum indicate a Blancan age (Tedford 1981).

The fossil specimen (NMMNH P-18816) represents a single individual, and consists of a braincase, 9 cervical vertebrae, 44 trunk vertebrae, 27 ribs (3 complete) and various fragments (Fig. 1). These bones were found slightly disarticulated and in close association. The trunk vertebrae lack hypapophyses, have relatively long and thin neural spines, are much longer than they are wide, and have thin and distinct hemal keels and vaulted neural arches. Based upon the work by Holman (1979), the above characteristics identify this fossil specimen as a colubrine.

The trunk vertebrae exhibit features characteristic of *Rhinocheilus lecontei* as enumerated by Hill (1971), namely flat zygosphenes in anterior view; obovate to oval prezygapophysial faces; thick neural spines (within the colubrines) that are also flat dorsally, overhanging centra posteriorly, with indented anterior and posterior edges; short centra, no epizygapophysial spines; depressed neural arches; round to
slightly compressed cotyla; postzygapophysial faces that are obovate to orbicular, strongly developed hemal keels and subcentral ridges, and swollen, very flat accessory processes. Holman (1979) recognized *Rhinocheilus* on the basis of trunk vertebrae that are almost equally long as wide, have strong subcentral ridges, and very long and thick accessory processes. These characters are evident in the fossil material. For these reasons this fossil specimen is assigned to the genus *Rhinocheilus*.

Hill (1971) and Holman (1979) noted that fossil specimens of *Rhinocheilus* from west Texas are indistinguishable from specimens of *R. lecontei* of Recent origin. A comparison of NMMNH P-18816 with a juvenile extant specimen of *R. lecontei* from the University of New
Mexico Museum of Southwestern Biology (UNM 47182) revealed that, except for size differences resulting from their differing ontogenetic stages, the two specimens were identical. Comparison of NMMNH P-18816 with a Recent specimen of *R. antoni* (UNM 41567), revealed major differences in the two specimens. The fossil specimen is not assigned to *R. antoni* due to the fact that the trunk vertebrae of the fossil specimen possess neural spines that are not strongly indented anteriorly and posteriorly, as well as articular facets that are broad, flat, and round in dorsal view.

Fossil specimens of *Rhinocheilus lecontei* have been reported from strata of Blancan age in Scurry County of west Texas (Rogers 1976) and from strata of Rancholabrean age in Kendall County of central Texas (Holman 1969a; 1969b; Hill 1971; Holman 1979). The present-day range of *Rhinocheilus* extends from California north to Nevada and south to Texas and Chihuahua (Wright & Wright 1957). This report of the New Mexican fossil of *Rhinocheilus* (1) represents the first record of a fossil snake from the late Cenozoic of New Mexico as well as the first fossil *Rhinocheilus* from the state; (2) extends the known range of fossil *Rhinocheilus* westward from Texas into central New Mexico; and (3) provides a much more complete fossil specimen of *Rhinocheilus* than those reported by Holman (1969a), Hill (1971) and Rogers (1976).

Acknowledgments

We wish to thank Bill Lang and Pete Reser for expert preparation of the fossil specimen and the Herpetology Division of the Museum of Southwestern Biology with the University of New Mexico for access to skeletons of extant *Rhinocheilus*, and two anonymous reviewers for their helpful comments.

Literature Cited


SATURN IN LATE 1993

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Abstract.—A combination of photometric and visual/photographic studies of the planet Saturn were conducted during September and October of 1993. Solar phase coefficients in mag./deg., of Saturn (globe+rings) measured through Johnson B, V, R and I filters were 0.055±0.007; 0.054±0.005; 0.047±0.010 and 0.053±0.007 respectively. The normalized magnitude of Saturn (excluding the rings) was V(1,0) = -8.84±0.04. Visual observations and photographs indicate that Saturn has returned to an appearance similar to that which was observed in 1989 prior to the occurrence of the large white storm of 1990.

Saturn attained opposition on 19 August 1993 and was at a declination of -15°. The ring plane was tilted at an angle of 12-13° with respect to the Earth in late 1993; this tilt is considerably less than 17° during 1992 and 20° during 1991. The changing tilt produces a change in the brightness of Saturn which can be photometrically measured. The changing aspect of Saturn’s rings may also provide additional information relative to the colors of Saturn and its rings. One of the primary objectives of observing Saturn during 1993 was to detect any changes in color, appearance or brightness which may have resulted due to the large white storm which occurred during 1990 (Barnet et al. 1992; Beebe et al. 1992; Benton 1992; Heath & McKim 1992).

This study provides data on the solar phase coefficients of Saturn (globe+rings) through the B, V, R and I filters along with normalized magnitudes extrapolated to a phase angle of zero degrees. The position, color and intensity of various atmospheric features of Saturn during late 1993 is also documented.

Photometric Methods

The 14 inch (36 cm) f/11 Schmidt-Cassegrain telescope at Texas A&M University Observatory was used during all measurements and observations. An Optec SSP-3 solid-state photometer was used with Johnson U, B, V, R and I filters during all photometric measurements. For additional information relative to the photometer and filters, refer to Optec (1988) and Schmude (1992).
The comparison star used during all measurements was γ-Cap. This star has respective U, B, V, R and I magnitudes of +4.20, +3.99, +3.67, +3.44 and +3.31 (Iriarte et al. 1965), and has coordinates (2000.0) of R.A. = 21h 40.09m and Dec. = -16° 39.75" (Hirshfeld & Sinnott 1985).

The measured magnitudes of Saturn along with other relevant information is listed in Table 1. All magnitudes have been corrected for atmospheric extinction. Both the solar phase angle of Saturn, \( \alpha \) and the tilt of the ring plane, B, were changing during the time period covered in Table 1.

The brightness of Saturn depends on \( \alpha \) and B according to:

\[
V(1,0) = V_{\text{meas}} - 5 \log gh - c \alpha + 2.60 \sin B - 1.25 \sin^2 B
\]

where \( V(1,0) \) is the normalized magnitude of Saturn without rings, \( V_{\text{meas}} \) is the measured V-filter magnitude of Saturn (globe + rings), \( g \) and \( h \) are the Saturn-Earth and Saturn-Sun distances in astronomical units, \( c \alpha \) is the solar phase angle coefficient in the V filter, \( \alpha \) is the solar phase angle of Saturn and B is the ring tilt. The "2.5 log k" term (where k is the fraction of the disc which is illuminated by the sun as seen from the Earth) is negligible for Saturn and is thus not included in the above equation.

The primary goal of the photometric study was to measure the solar phase angle coefficient, \( c \alpha \), of Saturn (globe + rings). Therefore, any change in brightness created by a changing B must be eliminated. The magnitude change, \( \Delta m \), of Saturn as a function only of ring tilt is reported (Harris, 1961) to obey:

\[
\Delta m = 2.60 \sin B - 1.25 \sin^2 B
\]

The value of \( \Delta m \) varied from 0.511 up to 0.528 during the time period covered in Table 1; therefore, in order to correct for \( B \) (or in other words, hold \( B \) constant), a scaling factor of \( 0.522 - \Delta m \) was subtracted from all normalized \( V(1,\alpha) \) values to obtain the \( V(1,\alpha) \)' values. The 0.522 is \( \Delta m \) when \( B=13.0^\circ \); the average value of \( B \) in Table 1.

The slope of the \( V(1,\alpha) \)' versus \( \alpha \) plot is 0.054 mag./deg. The slope, \( c \alpha \), is the solar phase coefficient of Saturn (globe + rings) in the V-filter when \( B=13^\circ \).

A similar procedure was used in the V filter measurements made in 1991 and the corresponding solar phase coefficient is listed in Table 2. The difference between the 1991 and 1993 solar phase coefficients is
Table 1. Summary of wideband photometric measurements made of Saturn in 1993. The solar phase angle is $\alpha$ and the ring tilt angle is $\beta$.

<table>
<thead>
<tr>
<th>Date (U.T.)</th>
<th>$\alpha$</th>
<th>$\beta$</th>
<th>Filter</th>
<th>Measured Magnitude</th>
<th>$X(1,\alpha)$</th>
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<td>+13.1°</td>
<td>V</td>
<td>+0.67</td>
<td>-9.10</td>
</tr>
<tr>
<td>Oct. 11.108</td>
<td>4.8°</td>
<td>+13.1°</td>
<td>R</td>
<td>+0.09</td>
<td>-9.68</td>
</tr>
<tr>
<td>Oct. 11.111</td>
<td>4.8°</td>
<td>+13.1°</td>
<td>I</td>
<td>+0.01</td>
<td>-9.76</td>
</tr>
<tr>
<td>Oct. 11.134</td>
<td>4.8°</td>
<td>+13.1°</td>
<td>U</td>
<td>+2.47</td>
<td>-7.30</td>
</tr>
<tr>
<td>Oct. 11.137</td>
<td>4.8°</td>
<td>+13.1°</td>
<td>V</td>
<td>+0.66</td>
<td>-9.11</td>
</tr>
<tr>
<td>Oct. 23.049</td>
<td>5.4°</td>
<td>+13.2°</td>
<td>U</td>
<td>+2.52</td>
<td>-7.29</td>
</tr>
<tr>
<td>Oct. 23.052</td>
<td>5.4°</td>
<td>+13.2°</td>
<td>B</td>
<td>+1.75</td>
<td>-8.06</td>
</tr>
<tr>
<td>Oct. 23.053</td>
<td>5.4°</td>
<td>+13.2°</td>
<td>V</td>
<td>+0.74</td>
<td>-9.07</td>
</tr>
<tr>
<td>Oct. 23.055</td>
<td>5.4°</td>
<td>+13.2°</td>
<td>R</td>
<td>+0.14</td>
<td>-9.67</td>
</tr>
<tr>
<td>Oct. 23.057</td>
<td>5.4°</td>
<td>+13.2°</td>
<td>I</td>
<td>+0.06</td>
<td>-9.75</td>
</tr>
<tr>
<td>Oct. 26.042</td>
<td>5.5°</td>
<td>+13.2°</td>
<td>B</td>
<td>+1.71</td>
<td>-8.11</td>
</tr>
<tr>
<td>Oct. 26.044</td>
<td>5.5°</td>
<td>+13.2°</td>
<td>V</td>
<td>+0.73</td>
<td>-9.09</td>
</tr>
<tr>
<td>Oct. 26.046</td>
<td>5.5°</td>
<td>+13.2°</td>
<td>R</td>
<td>+0.14</td>
<td>-9.68</td>
</tr>
<tr>
<td>Oct. 26.049</td>
<td>5.5°</td>
<td>+13.2°</td>
<td>I</td>
<td>+0.10</td>
<td>-9.72</td>
</tr>
<tr>
<td>Oct. 28.082</td>
<td>5.5°</td>
<td>+13.2°</td>
<td>B</td>
<td>+1.76</td>
<td>-8.06</td>
</tr>
<tr>
<td>Oct. 28.083</td>
<td>5.5°</td>
<td>+13.2°</td>
<td>V</td>
<td>+0.76</td>
<td>-9.07</td>
</tr>
<tr>
<td>Oct. 28.083</td>
<td>5.5°</td>
<td>+13.2°</td>
<td>R</td>
<td>+0.18</td>
<td>-9.64</td>
</tr>
<tr>
<td>Oct. 28.087</td>
<td>5.5°</td>
<td>+13.2°</td>
<td>I</td>
<td>+0.12</td>
<td>-9.70</td>
</tr>
</tbody>
</table>

believed to be real and due to the change in ring tilt. Solar phase coefficients are reported in Harris (1961) for the years 1914-15, 1917, 1918 and 1920; these values are listed in Table 2 along with the ring tilt (Nautical Almanac 1911; 1915a; 1915b; 1917). It appears that the solar
Table 2. Solar phase coefficients and normalized magnitudes measured for Saturn (globe + rings).

<table>
<thead>
<tr>
<th>Year</th>
<th>B</th>
<th>α-range</th>
<th>Filter</th>
<th>$c$ (mag./deg.)</th>
<th>$X(1,0)'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>+13°</td>
<td>3.2°-5.5°</td>
<td>B</td>
<td>0.055±0.007</td>
<td>-8.38</td>
</tr>
<tr>
<td>1993</td>
<td>+13°</td>
<td>3.2°-5.5°</td>
<td>V</td>
<td>0.054±0.005</td>
<td>-9.37</td>
</tr>
<tr>
<td>1993</td>
<td>+13°</td>
<td>3.2°-5.5°</td>
<td>R</td>
<td>0.047±0.010</td>
<td>-9.92</td>
</tr>
<tr>
<td>1993</td>
<td>+13°</td>
<td>3.2°-5.5°</td>
<td>I</td>
<td>0.053±0.007</td>
<td>-10.01</td>
</tr>
<tr>
<td>1992</td>
<td>+17°</td>
<td>5.2°-5.7°</td>
<td>V</td>
<td>9.45</td>
<td>a</td>
</tr>
<tr>
<td>1991</td>
<td>+20°</td>
<td>0.9°-5.7°</td>
<td>B</td>
<td>0.049±0.010</td>
<td>----</td>
</tr>
<tr>
<td>1991</td>
<td>+20°</td>
<td>0.9°-5.7°</td>
<td>V</td>
<td>0.038±0.007</td>
<td>-9.50</td>
</tr>
<tr>
<td>1920</td>
<td>-6°</td>
<td></td>
<td>---</td>
<td>0.049</td>
<td>----</td>
</tr>
<tr>
<td>1918</td>
<td>-17°</td>
<td></td>
<td>---</td>
<td>0.043</td>
<td>----</td>
</tr>
<tr>
<td>1917</td>
<td>-22°</td>
<td></td>
<td>---</td>
<td>0.033</td>
<td>----</td>
</tr>
<tr>
<td>1914-15</td>
<td>-27°</td>
<td></td>
<td>---</td>
<td>0.033</td>
<td>----</td>
</tr>
</tbody>
</table>

a Assuming a solar phase coefficient of 0.044 mag./deg.

b From (Harris 1961).

The solar phase coefficient increases with decreasing B (or increasing shadowing in the range $27° > B > 13°$). The increase in $c_v$ with decreasing B is consistent with the behavior of the Moon and Mercury. Essentially, as the shadowing of the Moon (Harris 1961) and Mercury (Veverka 1988) increases, the value of $c_v$ increases; likewise, as the shadowing of the rings increases, $c_v$ increases.

Determining the solar phase angle coefficients through the B, R, and I filters is more difficult because there is no equation available which relates $\Delta m$ to the ring tilt. For a close approximation, however, the same magnitude correction used for the V filter can be applied to the B, R and I filters. Such an approximation is reasonable since it is only the change in B, R and I magnitudes for ring tilt angles $12.7°-13.2°$ that is of interest. The resulting solar phase coefficients are listed in Table 2.

The normalized magnitude of Saturn calculated using the 1993 solar phase coefficient and the above first equation is $V(1,0)' = -8.84\pm0.03$ which is close to the accepted value of -8.88 (Nautical Almanac 1992; Harris 1961). The color indexes of Saturn (globe+rings) in 1993 at $B = 13°$ and $\alpha = 0°$ are: $B-V = +0.99\pm0.04$; $V-R = +0.55\pm0.04$ and $R-I = +0.09\pm0.04$. The uncertainties are estimated based on a combination of possible errors arising from star magnitude, atmospheric extinction, the above second equation and in the $V(1,0)'$ versus $\alpha$ plot.
Table 3. Summary of Saturnicentric latitudes of various features on Saturn. Feature abbreviations follow those of Schmude (1990).

<table>
<thead>
<tr>
<th>Feature</th>
<th>Reticle</th>
<th>Photograph</th>
<th>Video</th>
<th>Visual</th>
<th>Selected Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPR(^s)</td>
<td>56°N</td>
<td>57°N</td>
<td>-----</td>
<td>-----</td>
<td>57° ±4°N</td>
</tr>
<tr>
<td>NTB(^c)</td>
<td>44°N</td>
<td>38°N</td>
<td>-----</td>
<td>-----</td>
<td>35° ±5°N</td>
</tr>
<tr>
<td>NEB(^n)</td>
<td>26°N</td>
<td>27°N</td>
<td>21°N</td>
<td>26°N</td>
<td>25° ±2°N</td>
</tr>
<tr>
<td>NEB(^s)</td>
<td>16°N</td>
<td>16°N</td>
<td>13°N</td>
<td>15°N</td>
<td>15° ±2°N</td>
</tr>
<tr>
<td>X(^c)</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>9°N</td>
<td>9° ±4°N</td>
</tr>
<tr>
<td>STB(^c)</td>
<td>34°S</td>
<td>36°S</td>
<td>-----</td>
<td>35°S</td>
<td>35° ±3°S</td>
</tr>
</tbody>
</table>

Appearance of Saturn

The objective of this visual/photographic study was to determine the positions/colors of Saturn’s atmospheric features. A combination of visual and photometric studies should yield a more accurate picture of the overall behavior of Saturn.

Four different methods were used in measuring the Saturnicentric latitudes which are: visual, reticle, photograph and video measurements. Latitudes were computed from the formulae in Peek (1958) and the data in the Nautical Almanac (1992). The resulting latitudes are summarized in Table 3. In Table 3, NPR\(^s\)=south edge of the north polar cap; NTB\(^c\)=center of the north temperature belt, NEB\(^n\) and NEB\(^s\) are the north and south edges of the north equatorial belt respectively; STB\(^c\)=center of the south temperate belt and X\(^c\)=center of belt which is either the equatorial band or a portion of the north equatorial belt which split. The selected values are the equally weighted average of the values from the four methods. Uncertainties are estimated from: standard deviations, consistency between the different methods and visibility of the feature.

Between 1989 and 1991, the NEB appears to have moved northwards (Benton 1990; 1992; 1993; Heath 1992a; 1992b; 1993b; Schmude 1990), but this movement ceased during 1993. The 1993 position of the south temperate belt and the north polar region are consistent with those observed during the 1960s and 1970s (Hollis 1980).

The colors and intensities of the zones and belts of Saturn are listed in Table 4. The colors were estimated visually through the eyepiece and from color slides of Saturn. Kodak 100 HC color slide film was used
Table 4. Summary of intensity and color estimates of various atmospheric features on Saturn.

<table>
<thead>
<tr>
<th>Feature</th>
<th>Intensity</th>
<th>Color</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPR</td>
<td>4.2</td>
<td>Gray</td>
</tr>
<tr>
<td>NTZ</td>
<td>3.5</td>
<td>Yellow-gray</td>
</tr>
<tr>
<td>NTB</td>
<td>4.0</td>
<td>Brownish-gray</td>
</tr>
<tr>
<td>NTrZ</td>
<td>3.1</td>
<td>Yellow-gray</td>
</tr>
<tr>
<td>NEB</td>
<td>5.1</td>
<td>Brownish-gray</td>
</tr>
<tr>
<td>EZ</td>
<td>2.4</td>
<td>Yellow-white</td>
</tr>
<tr>
<td>STrZ</td>
<td>2.8</td>
<td>Yellow-white</td>
</tr>
<tr>
<td>STB</td>
<td>4.2</td>
<td>Gray</td>
</tr>
<tr>
<td>STZ</td>
<td>3.3</td>
<td></td>
</tr>
</tbody>
</table>

for all slides. Exposure times of 5-10 seconds were used at f/106 for the slides. Intensities were estimated on a scale from 0-bright white to 10-black using the same methods as reported by Schmude (1990). The colors and intensities, with the exception of the C ring, are similar to those in 1991 (Heath 1993; Benton 1993), 1990 (Heath 1992; Benton 1992) and 1989 (Benton 1990; Schmude 1990; Heath 1992). The consistency in colors and intensities is in agreement with the relatively constant photometric magnitudes of Saturn measured during 1991-1993.

The C ring was more distinct in 1993 than in the period 1987-1992. This may be due to the lower tilt of Saturn’s rings. According to McKim & Blaxall (1984), the contrast between the C ring and the black sky background increased as B decreased.

Discussion

The photometric results for Saturn in 1993 suggest that the solar phase coefficient depends on the tilt of the rings (angle B). The B-V color index for 1993 was $0.99 \pm 0.04$ which is a little lower than previous measurements (Nautical Almanac 1992; Harris 1961); this discrepancy may be due to the changing tilt of Saturn’s rings. In future studies, photometric measurements need to be carried out at different values of the ring tilt so that variations due to the rings can be determined. Only in this way can changes due to Saturn’s globe be detected using photometry. Definite statements about the globe of Saturn by itself thus can not be made until photometry of the rings is better understood. The major contribution of this work is that it adds to the current knowledge of the photometric behavior of Saturn’s rings.
Conclusions

In summary, a detailed photometric/photographic and visual study of Saturn was conducted during late 1993. Respective solar phase coefficients in the B, V, R and I filters were measured as: 0.055±0.007; 0.054±0.005; 0.047±0.010 and 0.053±0.007 in late 1993. It is concluded that the solar phase coefficient of Saturn (globe + rings) in the V-filter changes with respect to the ring tilt, B. A normalized magnitude of Saturn calculated from equation 1 and a solar phase coefficient of 0.054 mag./deg. is V(1,0)=-8.84. It is also concluded that the large white storm of 1990 did not create large changes in the color of Saturn in 1991-1993, but that a small shift in belt latitudes may have taken place.

References

A COMPARISON OF SIX TEST STATISTICS FOR DETECTING MULTIVARIATE NON-NORMALITY WHICH UTILIZE THE MULTIVARIATE SQUARED-RADII STATISTIC

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Hankamer School of Business, Baylor University, Waco, Texas 76798

Abstract.—This study presents tabulated empirically-derived critical values for Hawkins' test for non-normality, and compares the power of this test to five other test statistics designed to detect multivariate non-normality, all of which are functions of the multivariate squared-radii statistic. The power comparison has been accomplished using a Monte Carlo simulation with two sample sizes, two observation dimensions, and ten multivariate non-normal distributions. Among the six test statistics considered in the present study, the one proposed by Hawkins (1981) has proven to be the best omnibus test statistic for detecting multivariate non-normality. Empirically calculated critical values for Hawkins' test statistic for detecting multivariate non-normality are given as an appendix.

Strategies for testing the hypothesis of multivariate normality of a population from a set of sampled multivariate observations are numerous in the statistical literature. To date, over forty different test statistics have been recommended for this purpose. The interested reader is referred to thorough reviews by Gnanadesikan (1977), Mardia (1980), Koziol (1986), and Looney (1986). Attempts at detecting deviations from multivariate normality, using sample evidence from a set of multivariate observations, have typically employed one of the following strategies: (1) apply univariate techniques to detect marginal univariate non-normality for each dimension, (2) utilize multivariate techniques to detect joint non-normality, or (3) employ a univariate summary statistic to test for multivariate non-normality. Given a set of \( p \)-dimensional random variables \( X_1, X_2, \ldots, X_n \), the statistic most often utilized in testing for multivariate normality after the manner of strategy (3) is the squared sample radii statistic defined by

\[
D_i = (X_i - \overline{X}) S^{-1} (X_i - \overline{X})
\]

where

\[
\overline{X} = \frac{1}{n} \sum_{i=1}^{n} X_i \quad \text{and} \quad S = \frac{1}{n-1} \sum_{i=1}^{n} (X_i - \overline{X})(X_i - \overline{X})'.
\]

Several of the techniques designed to test the multivariate normality hypothesis have employed some variation of the multivariate squared radii statistic defined in (1). For example, Healy (1968) suggested that
the tables in Wilk et al. (1962) be used to construct a $\chi^2$ plot so that the multivariate normality hypothesis can be tested visually when $p = 2$. Malkovich & Afiffi (1973) proposed applying the Cramér-Von Mises and the Kolmogorov-Smirnov statistics to test the hypothesis that the values of $D_i$ have an approximate $\chi^2(p)$ distribution. For cases where $p \geq 2$, Small (1978) proposed plotting the order statistics of $D_i$ against the expected order statistics from a multiple of a beta distribution since, under the hypothesis of multivariate normality, the marginal distribution of $D_i$ is proportional to

$$
\frac{(n-1)^2}{n-1} \text{Beta} \left( \frac{p}{2}, \frac{(n-1)-p-1}{2} \right),
$$

where Beta $(a, b)$ denotes a beta distribution with shape parameters $a$ and $b$.

Another test procedure utilizing the squared-radii statistic has been formulated by Hawkins (1981) for simultaneously testing the assumption of multivariate normality of two or more sets of multivariate observations. He has proposed transforming the squared radii statistics into statistics with approximate $F$-distributions, assuming that multivariate normality of all data sets holds. He has shown that, under the assumption of multivariate normality, the tail probabilities will be distributed uniformly on the open unit interval. Hawkins suggested using the Anderson-Darling test statistic to test the assumption of uniformity for the transformed tail probabilities. Moore & Stubblebine (1981) proposed a multivariate normality test statistic which also is based upon the squared-radii statistic. The test statistic is of the form

$$
\chi^2 = \frac{1}{nk} \sum_{j=1}^{n} (kO_j - n)^2
$$

which has an approximate distribution of $\chi^2(q)$, $k - 1 \leq q \leq k$, where $O_i$ is the number of $D_i$, $i = 1,2,...,n$, whose values are in cell $j, j = 1,2,...,k$. One advantage of this statistic is that approximate critical values are easily obtained.

Fattorini (1982) proposed two statistics based on $D_i$ that may be used to test for multivariate non-normality. The first statistic is the average relative discrepancy among the sample order statistics and the expected order statistics from a multiple of the beta distribution. The second statistic utilizes the Theil index to measure the goodness of fit between
the sample order statistics and the expected order statistics from the beta distribution.

Koziol (1982) derived the asymptotic distribution of the Cramér-Von Mises type test of Malkovich and Afifi and also derived critical values via a Monte Carlo simulation for various sample sizes, dimensions, and significance levels. However, these critical values are not reported in the paper.

Royston (1983) formulated a test for multivariate normality based on the squared-radii statistic in which, assuming the hypothesis of multivariate normality, the squared-radii are transformed to near normality and then summed to form an approximate $\chi^2$ random variable.

Booker et al. (1984) noted that the $\chi^2(p)$ reference distribution used by Malkovich & Afifi (1973) in their Kolmogorov-Smirnov type test for multivariate normality could be improved by applying a multiple of the beta distribution as the reference distribution. However, the power of this test was examined for only the limited case of $p = 2$.

Paulson et al. (1987) proposed two tests for multivariate normality utilizing the squared-radii statistic. They find empirical critical values for dimensions one through five for an Anderson-Darling type statistic and they also formulate a test based on the Kullback divergence statistic.

Tsai & Koziol (1988) suggested using the Pearson correlation coefficient as a measure of the strength of the relationship between the order statistic for the squared-radii, $D_i$, and the approximate expected order statistics of the $D_i$ when assuming multivariate normality of the underlying population.

This paper compares the relative powers of six test statistics for detecting multivariate non-normality, all of which are functions of the squared-radii statistic. The power comparison is accomplished using a Monte Carlo simulation encompassing a variety of multivariate non-normal distributions. Additionally, a table of empirically-derived critical values for Hawkins’ test statistic for multivariate non-normality is constructed. Tabled critical values can be found in an appendix whilst a description of the simulation used to generate those critical values can be found in the next section along with a brief discussion of each of the six test statistics that are based on the squared-radii statistic and that have been compared in this study. Then, in Section 3, a brief description is given of the Monte Carlo simulation used for the power comparison and the results of that power comparison is presented.
Finally, in Section 4, comments on the simulation results are given and recommendations are made regarding the choice of a test statistic.

Six Test Statistics for Detection of Multivariate Non-Normality
Based upon the Squared-Radii Statistic

The goal of this study is the comparison of the powers of six test statistics designed to detect multivariate non-normality. Each of these statistics is a function of the squared-radii statistic defined in (1). For completeness a brief description of these test statistics is presented.

**Hawkins Test Statistic (HAW)**

Hawkins (1981) proposed a statistic for detecting multivariate non-normality which is a function of the squared-radii statistic, $D_i$. His procedure, which may be applied to observations from one or more populations simultaneously, is based upon a transformation of the squared-radii into statistics which have exact $F$-distributions under the assumption that the underlying populations are multivariate normal. If this assumption is true, the tail probabilities of the proposed statistic are distributed uniformly on the interval (0,1). The Anderson-Darling methodology is then employed to assess the uniformity of the tail probabilities. Hawkins’ test statistic for detecting multivariate non-normality of a single population may be described as follows. Let $D_i$ be defined as in (1) and let

$$F_i = \frac{(n-p-1)nD_i}{p(n-1)^2 - nD_i}.$$ 

Let $A_i = P[F > F_i]$ denote the tail area of a random variable with an $F$-distribution having $p$ and $(n - p - 1)$ degrees of freedom. Hawkins’ test statistic for detecting multivariate non-normality is based on the $n$ order statistics $A_{(1)} \leq A_{(2)} \leq \cdots \leq A_{(n)}$ of the $A_i$’s and may be written as

$$\text{HAW} = -n - \frac{1}{n} \sum_{j=1}^{n} (2j-1)[\log A_{(j)} + \log(1 - A_{(n-j+1)})].$$

Large values of HAW indicate a departure from the multivariate normal model. Note that this is nothing more than an application of the Anderson-Darling statistic to test uniformity of the $A_i$ values. Empirical critical values for Hawkins test statistic have been obtained via a Monte Carlo simulation that is described in the next section.
Empirically-derived Critical Values for Hawkins' Test Statistic

For each combination of sample size \( n = 10, 20, 30, 40, 50, 75, 100 \) and dimension \( p = 2, 3, 4, 5, 6, 8, 10, 12, 15 \), four sets of 5,000 sample observations of the statistic \( HAW \) have been generated from the \( p \)-dimensional standard normal distribution (i.e. a \( p \)-variate normal distribution with mean vector 0 and covariance matrix \( \Sigma = I \)). Notice that it will be sufficient to use the \( p \)-variate standard normal since the \( V_i \) are invariant under linear transformations. For each combination of \( n \) and \( p \), each set of 5,000 observations has been ordered and the appropriate sample quantile selected to estimate the critical value. The critical values that have been tabulated in the appendix, are actually the averages of the four sample quantiles for significance levels of 0.1, 0.05, 0.025, 0.01 and 0.005.

Computations have been performed on an IBM 4381 computer under the VM/CMS operating system in the Casey Computer Center at Baylor University. The code has been written in the SAS/IML software.

One further observation about the empirically generated critical values is worth mentioning here. A comparison of the asymptotic, Anderson-Darling critical values (recommended by Hawkins) and the empirically-derived critical values found in the appendix suggests that the asymptotic critical values may be quite conservative when applied to Hawkins' test statistic. Consider, for example, the case where \( n = 40, p = 5 \), and a significance level of .10 is adopted. Under these experimental conditions, the asymptotic critical value, which is independent of \( p \), is 1.933. A glance at the tabled empirical values in the appendix, however, reveals that the \( p \)-value corresponding to 1.933 is actually less than 0.005.

The Paulson-Roohan-Sullo Test Statistic (PRS)

The PRS test statistic was formulated by Paulson et al. (1987). This test statistic for detecting multivariate non-normality, like Hawkins' statistic, is based on the Anderson-Darling formulation. The PRS statistic may be expressed as

\[
PRS = -n - \frac{1}{n} \sum_{j=1}^{n} \left( 2j - 1 \right) \left( \log G(D_{(j)}) + \log[1 - G(D_{(n-j+1)})] \right)
\]

where \( G(\cdot) \) is the cumulative distribution of a \( \chi^2(p) \) random variable and \( D_{(j)} \) is the \( j \)th order statistic of the squared-radii statistic defined in (1). Note that Hawkins' test procedure differs from the PRS test procedure.
in that the latter statistic adopts a $\chi^2$-approximation for the $D_i$'s while the former test statistic utilizes a transformation of the $D_i$'s, resulting in tail probabilities with exact uniform distributions. Empirical critical values for the PRS statistic can be found in Paulson et al. (1987).

**The Tsai-Koziol Test Statistic (TK)**

The TK test statistic may be described as follows. Let $Q_1 \leq Q_2 \leq \ldots \leq Q_n$ denote the expected order statistics in a sample of size $n$ from a $\chi^2$-distribution with $p$ degrees of freedom. The Tsai-Koziol statistic, then, is of the form

$$TK = \frac{\sum_{i=1}^{n} (D_i - \bar{D})(Q_i - \bar{Q})}{\left[\sum_{i=1}^{n} (D_i - \bar{D})^2\right]^{1/2} \left[\sum_{i=1}^{n} (Q_i - \bar{Q})^2\right]^{1/2}}$$

where $\bar{D} = \frac{1}{n} \sum_{i=1}^{n} D_i$ and $\bar{Q} = \frac{1}{n} \sum_{i=1}^{n} Q_i$. Note that this statistic is nothing more than the Pearson correlation estimate for the correlation between the expected and empirical order statistics for the multivariate squared-radii statistic. The null hypothesis of multivariate normality is rejected for sufficiently small TK values. A selected group of sample critical values may be found in Tsai & Koziol (1988).

**The Extended Malkovich and Afifi Test Statistic (EMA)**

Malkovich & Afifi (1973) proposed another test statistic for detecting multivariate non-normality which is a function of the squared-radii statistic. Their statistic is essentially an extension of the Lilliefors statistic for testing univariate normality. The Malkovich and Afifi statistic is of the form

$$EMA = \sup_z \left| F_n(z) - G(z) \right|$$

where $F_n(z)$ is the sample cumulative distribution function of the squared-radii statistic and $G(z)$ is the cumulative distribution function of a $\chi^2(p)$ random variable. Concerning the performance of their test statistic, Malkovich and Afifi state "... a better approximation than $\chi^2(p)$ may be appropriate as the hypothetical distribution of $D_i$ ...." Jennings et al. (1990) applied a multiple of a beta random variable as an
approximation to the distribution of $D_i$. This statistic is of the form

$$EMA^* = \sup_z |F_n(z) - G^*(z)|$$

where $G^*(z)$ is taken to be a scaled Beta distribution. Note that this formulation is an extension of the statistic proposed by Booker et al. (1984) in the case where the dimensionality of the observation vectors is greater than two. Empirical critical values for this test statistic have been generated by Jennings et al. (1990).

*The Cramer-Von Mises Test Statistic (CM)*

Koziol (1982) derived a test statistic for detecting multivariate non-normality which is based on the Cramér-Von Mises distance measure between two distribution functions. This distance measure is of the form

$$\int_0^\infty [F(z) - G(z)]^2 dG_p(z)$$

where $F$ and $G$ are cumulative distribution functions. The Cramér-Von Mises test statistic formulated by Koziol (1982) is expressed as

$$CM = \frac{1}{12n} + \sum_{i=1}^n \left[ G(D_{i(i)}) - \frac{2j-1}{2n} \right]^2$$

where $G$ is the cumulative distribution function of a $\chi^2$ random variable with $p$ degrees of freedom. Unfortunately, Koziol (1982) includes only a limited number of empirical critical values.

*The Percent Mean Difference Test Statistic (PME)*

Fattorini (1982) suggested using the percent mean difference of the estimated quantiles of $D_i$ from the approximated expected quantiles of the squared-radii statistic assuming multivariate normality. The approximate expected quantiles of $D_i$ are calculated as functions of approximate beta quantiles of order

$$p_i = \frac{i-(a-1)/2a}{n-(a-1)/(2a) + 1},$$

$$h_i = \frac{i-(b-1)/2b}{n-(b-1)/(2b) + 1},$$
denoted by \( q_i \), where \( a = p/2 \) and \( b = (n - p - 1)/2 \). The expected quantiles for \( D_i \) may then be approximated by \( v_i = [(n - 1)^2/n]q_i \). The percent mean difference in the estimated quantiles, \( D_{(i)} \), and the approximate expected quantiles of \( D_i, v_i \), is then expressed as

\[
PME = \frac{1}{n} \sum_{i=1}^{n} \left| \frac{D_{(i)} - v_i}{v_i} \right|.
\]

Note that large values of PME indicate evidence of multivariate non-normality. Empirically derived critical values for selected sample sizes with dimensions 2 through 6 are given in Fattorini (1982).

The Simulation for Power Comparisons

To evaluate the relative powers of the six test statistics for detecting multivariate non-normality which are functions of the squared-radii statistic defined in (1), we conducted a Monte Carlo simulation using SAS/IML under the VM/CMS operating system on an IBM 4381. The simulation was performed in the following manner. Sets of ten thousand random vectors for sample sizes \( n = 20 \) and \( n = 50 \) from various nonnormal multivariate populations of dimensions \( p = 2 \) and \( p = 6 \) were generated. We evaluated each of the six test statistics using all possible configurations of sample size, dimension, and form of the nonnormal distribution.

The power study simulation made extensive use of the \( r \)-normed exponential distribution family which consists of symmetric, multivariate distributions. The reader may consult Goodman & Kotz (1973) or Chhikara & Odell (1973) for a complete discussion of this family. This study used multivariate \( r \)-normed exponential distributions with \( r = 1, 1.1, 1.2, 1.3, 1.4, 1.5, \) and \( 10 \). Other nonnormal distributions used in this study include four \( p \)-dimensional distributions with marginal \( \chi^2 \) variables having 1, 2, 3, and 4 degrees of freedom; and a \( p \)-dimensional distribution with marginal uniform variates.

The non-normality of these distributions was assessed using multivariate measures of skewness and kurtosis formulated by Mardia (1970). The multivariate skewness measure is

\[
\beta_{1,p} = \sum_{i,j,k=1}^{p} \sum_{e,f,g=1}^{p} \sigma_{ie} \sigma_{if} \sigma_{ig} \mu_{111}^{(i,j,k)} \mu_{111}^{(e,f,g)}.
\]
and the multivariate kurtosis measure is

$$\beta_{2,p} = \sum_{i,j=1}^{p} \sum_{k,l=1}^{p} \sigma_{ij} \sigma_{kl} \mu_{ijkl}^{(ijkl)},$$

where

$$\mu_{ijkl}^{(ijkl)} = \text{E}(X_i - \mu_i)^{r}(X_j - \mu_j)^{s}(X_k - \mu_k)^{t}(X_l - \mu_l)^{u}).$$

and $\Sigma^{-1} = (\sigma_{ij})$ for $i,j = 1,\ldots,p$. Mardia (1970) showed that $\beta_{1,p} = 0$ and $\beta_{2,p} = p(p+2)$ for multivariate normal distributions. It is noted, here, that there are many types of non-normality and that Mardia's measures of multivariate skewness and kurtosis do not characterize all of them.

Empirical powers were calculated as the proportion of rejections at both the $\alpha = 0.10$ and the $\alpha = 0.05$ levels of significance. Empirically-generated critical values (based upon 10,000 samples) are employed for all test statistics in the interest of equitable power comparison.

**Power Simulation Results**

The results of our power comparison (for $\alpha = 0.10$) is given in Figure 1. Each pair of histograms in the figure shows the powers of the six test statistics for both sample sizes ($n = 20$ or $n = 50$) when $p = 2$ (graph on left) or 6 (graph on right). When $\alpha = 0.05$, the powers of all tests, naturally, are smaller compared to $\alpha = 0.10$. The relative performances of the tests, however, are unaffected by the choice of $\alpha$ (0.10 or 0.05) for each experimental combination of $n$, $p$, and type of non-normality examined. In the interest of brevity, therefore, we have not presented the results for $\alpha = 0.05$.

Careful examination of each of the graphs in Figure 1 reveals that no test statistic is uniformly most powerful over all of the configurations considered in the simulation study. Indeed, the results presented here give us reason to reiterate, albeit less vigorously, the recommendations of Andrews, Gnanadesikan, & Warner (1973:95) who advise that "...a variety of techniques with differing sensitivities to the different types of departures" should be used when testing for multivariate non-normality. In the subsections that follow, we comment on the "sensitivity" and
relative performance of each of the test statistics examined over the various combinations of \( n, p \), and type of non-normality.

**Hawkins Test Statistic (HAW)**

Hawkins’ statistic yields excellent power characteristics for many of the distributions considered in this study. This test statistic has, for example, excellent power against both symmetric, heavy-tailed and skewed distributions regardless of the sample size or dimension. From the graphs in Figure 1, it is clear that Hawkins’ test statistic very often enjoys increased statistical power when the dimension is expanded from 2 to 6, for both sample sizes. In contrast, all but one of the competing statistics tended to lose power as the dimension was increased, especially with small samples (\( n=20 \)). The one exception is the PME statistic which we describe in more detail below. Hawkins’ statistic does not, however, exhibit high power against symmetric light-tailed distributions and, in fact, the comparatively poor power of Hawkins’ test for these types of distributions worsens with increasing dimension.

**Percent Mean Difference Test Statistic (PME)**

Fattorini’s PME test statistic also exhibits good power against skewed and symmetric, heavy-tailed distributions. For all of these types of non-normality, however, the power of the PME statistic declined markedly when the dimension is reduced from 6 to 2. This phenomenon is especially noticeable with small samples (\( n=20 \)). The practical implication, here, is that while the statistic’s relative performance is good for skewed and symmetric, heavy-tailed distributions, that performance depends in large part upon the ratio, \( n/p \), and suffers greatly when this ratio is large. In addition, the PME statistic, like Hawkins’ statistic, has relatively poor power against symmetric, light-tailed distributions. There is little reason, then, to recommend the PME statistic over Hawkins’ statistic unless the non-normality is likely to be in the form of very heavy-tailed distributions and the ratio, \( n/p \), is quite small.

**Paulson-Roohan-Sullo Test Statistic (PRS)**

The PRS test statistic provides superior power only on those occasions where the non-normality manifests itself in the form of symmetric, light-tailed distributions. Results presented in Figures 1, however, do demonstrate that on such occasions, the PRS test statistic has markedly better relative power than all but one other statistic (see CM below). The
practical implication is that this statistic is most powerful in situations where Hawkins’ test and the PME statistic provide relatively poor performances. The reader is cautioned, however, that both the PRS and CM statistics have relatively poor power against skewed and symmetric, heavy-tailed distributions. Indeed, on some occasions the powers of these tests can be smaller than the actual level of the test (i.e. against symmetric, medium to heavy-tailed distributions where the ratio of the sample size to dimension is relatively small \((n/p < 4)\)). Thus, the PRS and CM test statistics biased tests for detecting multivariate non-normality.

**Tsai-Koziol Test Statistic (TK)**

In terms of statistical power, the TK test statistic proves to be markedly inferior to nearly all of the other test statistics except on two occasions where the ratio of sample size to dimension was large and the non-normality occurred in the form of moderately skewed distributions. There is little reason to consider this statistic in the data analytic setting or in any future research efforts.

**Cramer-Von Mises Test Statistic (CM)**

The CM statistic, like the PRS test statistic enjoys power advantages only on those occasions characterized by symmetric, light-tailed distributions. Even then, the power of the CM statistic is less than that of the PRS statistic. Both of these statistics are inferior to nearly all other tests examined when attempting to detect multivariate non-normality in the form of heavy-tailed or skewed distributions. Finally, there is little reason to prefer CM to PRS when choosing a test that will be sensitive to symmetric, light-tailed forms of non-normality.

**Extended Malkovich and Afifi Test Statistic (EMA)**

The EMA statistic enjoys adequate relative power against skewed and symmetric, heavy-tailed distributions, typically ranking third (after Hawkins and PME) in order of relative power for these experimental conditions. The EMA statistic does enjoy power advantages over all other tests, on those occasions where the nonnormal distribution is extremely skewed and the ratio of sample size to dimension is quite large. However, under these conditions all of the tests have reasonably large powers and any power differences are likely to be inconsequential. Incidentally, the EMA statistic also gives a relatively poor performance
against multivariate non-normality in the form of light-tailed distributions.

Conclusions

This study compares the relative powers of six test statistics (all of which are functions of the squared-radii statistic) that can be used to detect multivariate non-normality. While none of the statistics considered here was most powerful against all of the alternative distributions simulated, Hawkins' test statistic appears to have relatively good power against many of the types of multivariate non-normality considered in the present study. This is especially true of non-normality in the form of skewed or heavy-tailed distributions. Even on those occasions when Hawkins' test statistic does not yield superior power (for symmetric, light-tailed distributions), the power is fairly good in that the power differences between Hawkins' test and the "best" test statistic never exceeds about .10. It is also worth mentioning that Hawkins' test statistic is one of a few tests examined here that benefits (enjoys increased power) from increases in the dimension with no associated increases in sample size. Additionally, Hawkins' test statistic is not difficult to compute and is readily applied in the research setting.

Two cautionary notes on applying Hawkins' test statistic is in order. If the ratio of the sample size $n$ to the dimension $p$ is too small, the statistic $H$, can be negative and, therefore, useless. Simulation results indicate that this condition can usually be avoided if care is taken to insure that the ratio of sample size to dimension will be greater than or equal to 2. Also, in his paper Hawkins (1981) uses asymptotic critical values for an example application and states that the asymptotic critical values seem to be adequate. Unfortunately, this study reveals that the asymptotic critical values suggested by Hawkins (1981) yield test levels that differ considerably from the assumed test levels using asymptotic critical values. As noted in Section 2 critical values for Hawkins' statistic have been tabulated and are given in the appendix.

Literature Cited


Figure 1. Powers of the Six Test Statistics for

\[ N=20 \quad \text{and} \quad N=50 \quad \alpha = 0.10 \]

\( p=2 \)

- \( X^2(3): \beta_{12}=5.33 \quad \beta_{13}=16.00 \)
  - HAW: 0.491
  - PME: 0.425
  - PRS: 0.133
  - TK: 0.239
  - CM: 0.124
  - RMA: 0.405

- \( X^2(4): \beta_{12}=4 \quad \beta_{13}=14.00 \)
  - HAW: 0.371
  - PME: 0.331
  - PRS: 0.108
  - TK: 0.274
  - CM: 0.090
  - RMA: 0.307

\( p=6 \)

- \( X^2(3): \beta_{14}=16 \quad \beta_{15}=72.00 \)
  - HAW: 0.895
  - PME: 0.868
  - PRS: 0.774
  - TK: 0.768
  - CM: 0.807
  - RMA: 0.859

- \( X^2(4): \beta_{14}=12 \quad \beta_{15}=66.00 \)
  - HAW: 0.801
  - PME: 0.755
  - PRS: 0.618
  - TK: 0.664
  - CM: 0.662
  - RMA: 0.741

\( \text{Uniform: } \beta_{12}=8 \quad \beta_{13}=8 \)

- HAW: 0.366
- PME: 0.378
- PRS: 0.446
- TK: 0.209
- CM: 0.477
- RMA: 0.263

\( \text{Uniform: } \beta_{14}=0 \quad \beta_{15}=0 \)

- HAW: 0.886
- PME: 0.896
- PRS: 0.945
- TK: 0.219
- CM: 0.758
- RMA: 0.929
Figure 1. Powers of the Six Test Statistics for

\[ N = 20 \quad N = 50 \quad \alpha = 0.10 \]

\( p = 2 \)

\( p = 6 \)

\[ \text{MEP}(r=1.0): \beta_{12} = 0 \quad \beta_{22} = 14.00 \]

\[ \text{HAW: } 0.482 \quad \text{PME: } 0.416 \quad \text{PRS: } 0.405 \quad \text{TK: } 0.249 \quad \text{CM: } 0.378 \quad \text{RMA: } 0.456 \]

\[ \text{MEP}(r=1.1): \beta_{12} = 0 \quad \beta_{22} = 12.55 \]

\[ \text{HAW: } 0.405 \quad \text{PME: } 0.343 \quad \text{PRS: } 0.326 \quad \text{TK: } 0.203 \quad \text{CM: } 0.300 \quad \text{RMA: } 0.380 \]

\[ \text{MEP}(r=1.2): \beta_{12} = 0 \quad \beta_{22} = 11.48 \]

\[ \text{HAW: } 0.333 \quad \text{PME: } 0.272 \quad \text{PRS: } 0.263 \quad \text{TK: } 0.183 \quad \text{CM: } 0.244 \quad \text{RMA: } 0.312 \]

\[ \text{MEP}(r=1.0): \beta_{12} = 0 \quad \beta_{22} = 66.00 \]

\[ \text{HAW: } 0.916 \quad \text{PME: } 0.921 \quad \text{PRS: } 0.793 \quad \text{TK: } 0.371 \quad \text{CM: } 0.714 \quad \text{RMA: } 0.802 \]

\[ \text{MEP}(r=1.1): \beta_{12} = 0 \quad \beta_{22} = 61.65 \]

\[ \text{HAW: } 0.833 \quad \text{PME: } 0.833 \quad \text{PRS: } 0.589 \quad \text{TK: } 0.289 \quad \text{CM: } 0.568 \quad \text{RMA: } 0.689 \]

\[ \text{MEP}(r=1.2): \beta_{12} = 0 \quad \beta_{22} = 58.46 \]

\[ \text{HAW: } 0.719 \quad \text{PME: } 0.719 \quad \text{PRS: } 0.500 \quad \text{TK: } 0.427 \quad \text{CM: } 0.564 \]
Figure 1. Powers of the Six Test Statistics for

\[ N=20 \quad N=50 \quad \alpha = 0.10 \]

- MEP (r=1.3): \( \beta_{1,2}=0 \) \( \beta_{2,2}=10.67 \)
- MEP (r=1.4): \( \beta_{1,2}=0 \) \( \beta_{2,2}=10.30 \)
- MEP (r=1.5): \( \beta_{1,2}=0 \) \( \beta_{2,2}=9.52 \)

- MEP (r=1.3): \( \beta_{1,6}=0 \) \( \beta_{2,6}=56.02 \)
- MEP (r=1.4): \( \beta_{1,6}=0 \) \( \beta_{2,6}=54.10 \)
- MEP (r=1.5): \( \beta_{1,6}=0 \) \( \beta_{2,6}=41.30 \)
Figure 1. Powers of the Six Test Statistics for

$p=2$

$N=20$

$N=50$

$\alpha = 0.10$

$p=6$

**MEP**
- $r=10$: $\beta_{1,2}=0 \quad \beta_{2,2}=0.18$
- $0.767 \quad 0.303$
- $0.798 \quad 0.369$
- $0.829 \quad 0.414$
- $0.845 \quad 0.601$

**HAW**
- $0.912$
- $0.803$
- $0.681$
- $0.504$

**PME**
- $0.210$
- $0.325$
- $0.587$
- $0.397$

**PRS**
- $0.458$
- $0.174$
- $0.439$
- $0.397$

**TK**
- $0.177$
- $0.174$
- $0.417$
- $0.485$

**CM**
- $0.379$
- $0.398$
- $0.240$
- $0.505$

**RMA**
- $0.178$
- $0.211$
- $0.505$
- $0.505$

**X1**
- $\beta_{1,2}=16 \quad \beta_{2,2}=32.00$
- $0.995$
- $0.999$
- $0.999$

**X2**
- $\beta_{1,2}=8 \quad \beta_{2,2}=20.00$
- $0.889$
- $0.639$
- $0.605$

**X3**
- $\beta_{1,2}=24 \quad \beta_{2,2}=84.00$
- $0.898$
- $0.896$
- $0.953$

**POWER**
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**Appendix.** Approximate upper .10, .05, .025, .001 and .0005 level critical values for Hawkins' Test for multivariate normality of a single distribution.
VOMEROFACTORY EXPLORATION OF NOVEL ENVIRONMENTS BY THE PARTHENOGENETIC WHIPTAIL LIZARD *CNEMIDOPHORUS LAREDOENSIS* (SAURIA: TEIIDAE)

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*Department of Biological and Environmental Sciences, McNeese State University, Lake Charles, Louisiana 70609*

**Abstract.**—The frequency rate of tongue touch behavior of the whiptail lizard *Cnemidophorus laredoensis* was observed in the laboratory to determine the nature of this activity when exposed to a variety of different environmental habitats. This study reveals that *C. laredoensis* increases vomerolfactory exploration equally in all novel environments but, unlike other species of lizards, may be unable to distinguish among different novel odors.

Many studies have shown that lizards are capable of detecting ecologically relevant odors (see reviews by Simon 1983; Cooper 1994). In addition, many species are capable of detecting odors of conspecifics and/or heterospecifics (DeFazio et al. 1977; Duvall 1979; Duvall et al., 1980; Bissinger & Simon 1981; Cooper & Vitt 1987). Studies of tongue flick rates (Bissinger & Simon 1979) and responses to prey odors (Cooper 1990; Cruz-Neto & Andrade 1993) indicate that members of the lizard family Teiidae exhibit well developed vomerolfaction (sensu Cooper & Burghardt 1990). While vomerolfaction may also play a role in species identification and detection of conspecifics in teiids (Carpenter 1962; Simon 1983), this premise has never been tested.

The Laredo striped whiptail, *Cnemidophorus laredoensis*, is a parthenogenetic teiid lizard which occurs in the sandy disturbed habitats in and near the Rio Grande Valley of Texas and Mexico (Walker 1987). It arose from hybridization between the bisexual species *C. gularis* and *C. sexlineatus* (cf. McKinney et al. 1973; Bickham et al. 1976; Wright et al. 1983). Most habitat sites occupied by *C. laredoensis* are also occupied by *C. gularis* (cf. Paulissen et al. 1992). Both species forage for arthropods by moving widely through the habitat while rapidly flicking the tongue; both also use small burrows for overnight retreats (Walker et al. 1986; Paulissen et al. 1988). When a specimen of *C. laredoensis* forages, it moves away from the vicinity of its burrow and will consequently encounter a variety of novel vomerolfactory stimuli such as odors left on the ground by conspecifics or *C. gularis*. Specimens may alter their exploratory behavior in novel environments to gain information relative to the presence of other lizards in the
immediate area. This study analyzes tongue touch rates of captive *C. laredoensis* to determine the extent that this species uses the tongue to chemically sample novel environments.

**Methods and Materials**

Nine adult specimens of *Cnemidophorus laredoensis* (=clonal complex LAR-A; Walker 1986; 1987) and four adult specimens of *C. gularis* were collected in Cameron and Hidalgo counties in south Texas. Specimens were housed individually in 10-gallon (36 by 50 by 31 cm) terraria provided with 3 cm of clean sand, a water dish, and a 5 by 6 cm piece of cardboard for shelter. Each terrarium was heated with a 60 watt lamp placed against the side of the terrarium; overhead fluorescent lights connected to timers simulated mid-summer photoperiod (day length of 14 hr). Each specimen was fed 2-3 mealworms a day and water was provided as needed.

Specimens were tested in a terrarium of above dimensions containing soiled sand and a cardboard shelter and heated by a 60 watt lamp. Each specimen was tested in six different odor environments: resident odor (simulating the test specimen’s home environment), conspecific odor (of another *C. laredoensis*), congeneric male odor (of male *C. gularis*), congeneric female odor (of female *C. gularis*), non-saurian odor (no lizard odor), and artificial odor (perfume - Avon’s Knowing). To create the resident odor environment, the test lizard was placed in the test terrarium and left for 24 hours. The specimen was then removed for a few seconds, returned to the test terrarium, and observed. To create the environments with odors of another *C. laredoensis* or a *C. gularis*, a lizard was placed into the test terrarium and left for 24 hours after which it was removed and replaced with the test lizard. The environment of non-saurian odor was created by using a terrarium that had not been previously occupied. The artificial odor environment was created by spraying clean sand with perfume just before testing began. Each specimen was exposed to the six odor environments in random order. The cardboard shelter was removed just prior to testing to prevent the test lizard from escaping from the observer’s view.

Data were collected by placing a test lizard in a test terrarium and observing it for 20 minutes. The following were measured: (1) number of tongue touches (i.e. extrusions of the tongue onto the sand or glass of the terrarium); (2) time the specimen spent moving (as opposed to basking in front of the light) measured in minutes with a stopwatch; (3)
number of tongue touches per minute while the specimen was moving about in exploratory fashion (to account for the fact that the room temperature varied slightly among experiments causing lizards to spend varying amounts of time basking). Differences between odor environments were statistically evaluated by analysis-of-variance and Duncan's multiple range tests (SAS Institute 1985).

Upon being placed in a test terrarium specimens initially remained stationary for several minutes; they would then begin moving about in the terrarium while rapidly touching the tongue to the sand. After a few minutes the specimen typically basked in front of the heat lamp for a short time; specimens were not observed to tongue touch while basking. When the specimen resumed moving, its behavior consisted of tongue touching, digging, and pushing its nose against the glass or trying to climb out. This alteration of moving and basking continued until the end of the 20 minute testing period.

Results and Observations

The mean number of tongue touches and time spent moving were significantly lower in the resident odor environment versus the other odor environments, and the number of tongue touches per minute was significantly higher than for the other odor treatments (Table 1). When specimens were tested in their resident odor environment, they moved about and rapidly tongue touched for short amounts of time primarily during the first half of the test period. The rest of the time was spent near the heat lamp. When placed in any of the novel odor environments, specimens were observed to spend less time basking and more time moving. Moving involved not only tongue touches, but also attempts to escape (i.e. climbing up the glass, pushing nose against the glass, and digging in the sand). Specimens were much more active in the novel environments and rested only after being away from the heat of the lamp for several minutes. This behavior of alternating basking and trying to escape continued throughout the entire test period.

The results of this experiment suggest that specimens of *Cnemidophorus laredoensis* increase vomerolfactory exploration in novel or unfamiliar environments. Presumably, this potentially allows them to detect novel or unfamiliar areas or burrows. Field observations appear to support this premise. When a specimen of *C. laredoensis* encounters several burrow entrances in the field, it rapidly tongue touches at first one, then another before finally entering a burrow. These observations suggest that *C. laredoensis* may be using vomerolfaction to locate their
Table 1. Mean (x) and standard deviation (SD) of vomerolfactory exploration measures for *Cnemidophorus laredoensis* exposed to six different odor environments for 20 minutes. Results that are significantly different from all other results are indicated by an asterisk (ANOVA Duncan’s multiple-range tests; P < 0.05). Sample size was nine lizards for each odor environment.

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<tr>
<th>Odor Environment</th>
<th>Number of Tongue Touches</th>
<th>Time Spent Moving (Min)</th>
<th>Tongue Touches/Min While Moving</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x = 114.7*</td>
<td>x = 5.1*</td>
<td>x = 23.4*</td>
</tr>
<tr>
<td>Resident Odor</td>
<td>SD = 52.0</td>
<td>SD = 2.1</td>
<td>SD = 7.4</td>
</tr>
<tr>
<td>Conspecific Odor</td>
<td>x = 209.2</td>
<td>x = 12.1</td>
<td>x = 17.7</td>
</tr>
<tr>
<td>SD = 40.4</td>
<td>SD = 2.6</td>
<td>SD = 3.8</td>
<td></td>
</tr>
<tr>
<td>Congeneric Male Odor</td>
<td>x = 203.3</td>
<td>x = 11.1</td>
<td>x = 18.8</td>
</tr>
<tr>
<td>SD = 45.6</td>
<td>SD = 3.0</td>
<td>SD = 3.6</td>
<td></td>
</tr>
<tr>
<td>Congeneric Female Odor</td>
<td>x = 193.4</td>
<td>x = 11.4</td>
<td>x = 17.1</td>
</tr>
<tr>
<td>SD = 30.9</td>
<td>SD = 1.9</td>
<td>SD = 2.2</td>
<td></td>
</tr>
<tr>
<td>Non-saurian Odor</td>
<td>x = 201.1</td>
<td>x = 12.9</td>
<td>x = 15.7</td>
</tr>
<tr>
<td>SD = 30.5</td>
<td>SD = 2.2</td>
<td>SD = 1.9</td>
<td></td>
</tr>
<tr>
<td>Artificial Odor</td>
<td>x = 211.6</td>
<td>x = 12.3</td>
<td>x = 18.1</td>
</tr>
<tr>
<td>SD = 29.7</td>
<td>SD = 3.2</td>
<td>SD = 4.3</td>
<td></td>
</tr>
</tbody>
</table>

own individual retreats and/or avoid burrows occupied by other lizards. This behavioral pattern may serve to minimize contact with conspecifics and so reduce intraspecific competition. Also, it may aid in avoiding male specimens of *C. gularis* which occasionally copulate with *C. laredoensis* to produce hybrids that are morphologically and genetically different from the parthenogens (Walker et al. 1989).

Conclusions

This study reveals that specimens of *C. laredoensis* exhibit the same tongue-touch rates in all five of the novel odor environments tested (Table 1). This contrasts with the studies of other lizards such as *Sceloporus jarrovi* which was reported to tongue touch significantly less frequently in a clean cage (i.e. no odor treatment) than in a cage previously occupied by a conspecific (DeFazio et al. 1977; Bissinger & Simon 1981). The fact that *C. laredoensis* exhibits the same tongue touch rate in different novel environments suggests that either it responds to any novel environment with the same elevation of tongue touch rate or is unable to distinguish among different novel odors.
Acknowledgments

We wish to thank M. Wygoda, G. Haigh, and three reviewers for providing constructive comments on this manuscript. Laboratory space and equipment were provided by the Department of Biological and Environmental Sciences, McNeese State University. Specimens were collected under the authority of scientific collecting permit no. SPR-0691-408 granted by the Texas Parks and Wildlife Department to M. A. Paulissen. This study is the result of a Senior Honor’s thesis conducted by L. R. Rybiski.

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HABITAT USE OF INTRODUCED AND NATIVE ANOLES (IGUANIDAE: ANOLIS) ALONG THE NORTHERN COAST OF JAMAICA

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Abstract.—A comparison of the spatial distribution of the introduced Anolis sagrei with the native Anolis grahami and Anolis lineatopus was conducted along the north coast of Jamaica during the spring of 1983, 1987 and 1994. Spatial distribution was determined as a product of perch height and perch diameter. Perch heights differed significantly among the three species. Due to the presence of considerable overlap in the two niche dimensions, these variables were natural log transformed to construct a two-dimensional niche space to view species overlap. Anolis sagrei is an invader that has apparently integrated into the native Anolis community at this locality. The results of this study are discussed regarding implications for coexistence and potential competition between these three species of anoles.

Community structure may arise by both rapid processes occurring in ecological time as well as by more long term processes acting over evolutionary time (Roughgarden et al. 1983; Grant 1986). Communities may be structured through mutual co-adaptation of community members, or by invaders. For an invading species to be successful as a colonist, it must be pre-adapted to integrate in with other members of the community (Rummel & Roughgarden 1983; 1985). Caribbean anoles provide good model systems for analyzing community structure due to their relative simplicity. The extent to which such communities are the result of coevolution among species, however, remains ambiguous (Williams 1972; Roughgarden 1989; Losos 1992a; 1992b). Investigation into the effects of the invasion by the introduced Anolis sagrei may provide some degree of insight into the evolution of Anolis communities within the Caribbean area.

The purpose of this study was to examine the spatial niche or structural habitat of three common species of anoles (Anolis grahami, A. sagrei and A. lineatopus) along the northern coast of Jamaica. For a complete description of the three species, refer to Underwood & Williams (1959). Four site localities were chosen for the ease of long term sampling and due to the fact that the flora of each is typical of the area. The "structural habitat" (Rand 1964) of an Anolis species refers to both the flora and other objects upon which these arboreal lizards are found. Rand (1964) originally used perch height and perch diameter to
distinguish the spatial niche dimensions utilized by anole species. Other authors (Schoener 1967; Schoener & Schoener 1971; Losos et al. 1993) have also used these measures to quantify habitat use. Spatial habitat use has also been described by perch type and by the degree of insolation (Schoener & Schoener 1971; Loses et al., 1993). Perch height and perch diameter may be the most conveniently quantified measures of structural habitat. This is because these characteristics are correlated with other habitat features and if partitioned between or within species will allow a large number of lizard species to coexist in a relatively small area. For example, in studying five species of anoles at three lowland localities in Jamaica, Schoener & Schoener (1971) found that the anoles had partitioned their spatial niches to reduce spatial overlap and avoid potential intraspecific and interspecific competition. However, such measures may not accurately represent the total niche usage by the community fauna.

*Anolis sagrei* is an invader that is expanding its range across the island of Jamaica (Underwood & Williams 1959; Williams 1969; Mayer 1989), and it is reasonable to expect changes in the anole community. This study was designed to quantify perch height and perch diameter, and compare these distributions among the species. It also examines spatial overlap of these dimensions with plots of habitat space.

**Materials and Methods**

Observations were made at the Hofstra University Marine Laboratory campus at Priory, Saint Ann’s Parish, Jamaica. The data were collected on March 10-13, 1983, March 10-13, 1987, and January 4-7, 1994 between 0830-1800 hours from four selected study sites on the campus. Study sites included a beach and three highly disturbed areas. The disturbed areas included laboratory buildings, concrete walls, telephone poles, a barb wire fence, lumber and brick piles, and a low wooden pier. Flora present in all of these areas included red mangrove, coconut, banana trees, and several varieties of cultivated garden plants. Potential habitat availability was similar in all of the selected study sites.

Each study site was carefully examined by one or two observers several times during the day. When an anole specimen was observed, its perch height and perch diameter were recorded by tape measure to the nearest cm. Specimens observed on the ground or on walls were assigned a perch height of zero. Only large adult males were used in the study due to the fact that they are larger and more conspicuous due to their social dewlap displays. Several other studies on anoles have
Figure 1. Frequency histogram of recorded perch heights for: (a) *Anolis grahami* (N = 197, six points above 6 m were excluded), (b) *Anolis sagrei* (N = 164), (c) *Anolis lineatopus* (N = 76).
focused exclusively on adult males (Rand & Williams 1969; Williams 1972; 1983).

Mean perch heights and perch diameters were calculated for all study sites for all three years. Perch heights were compared using Kolmogorov-Smirnov Two-sample tests (two-tailed). When the same data were used in pairwise multiple comparisons, the sequential Bonferroni technique (alpha = 0.05) was used to judge statistical significance (Rice 1989). Probabilities reported remain significant with the Bonferroni correction. Also, habitat space plots were constructed from natural log transformed data of perch height and perch diameter to compare overlap in these niche dimensions.

Results

The frequency distributions of perch heights for each species during all years of the study are graphed in Figure 1. Komolgorov-Smirnov Tests indicate statistically significant differences in perch heights among all three species during all years of the study ($A. grahami$ vs. $A. sagrei$ $D = 42.57, n = 197, 164, P<0.001$; $A. grahami$ vs. $A. lineatopus$ $D = 22.23, n = 197,76, P<0.001$; $A. lineatopus$ vs. $A. sagri$ $D = 14.15, n = 76,164, P<0.001$).

Highly statistically significant differences were found to exist among species in these niche dimensions. Yet, habitat space plots revealed that there is substantial overlap in both perch heights and perch diameters among all three species during the study (Figure 2). The largest overlap in these measures of habitat use was found between the invading species $A. sagrei$, and the resident species $A. lineatopus$. $Anolis grahami$ tended to occupy the highest and largest diameter perches when compared to the other two species studied.

Discussion

The results of this study indicate that there are statistically significant differences among these three species in perch heights, even though our space plots reveal that there is still considerable overlap on these niche axes. Because of this result, it would be useful then to examine other niche axes to determine the coexistence of these species. Statistical differences in perch heights may not be biologically meaningful measures of habitat use due to the fact that they do not adequately or accurately represent the lizard’s structural niche. Other measures such as degree of insolation, and/or finer scale habitat measures may be
Figure 2. Scatterplot of perch height vs. perch diameter for: (a) *Anolis grahami* (N = 197), (b) *Anolis sagrei* (N = 164), (c) *Anolis lineatopus* (N = 76).
needed to more adequately quantify habitat use.

Questions arise as to the nature of the factors which allow these species to coexist. There may be ecological differences among these species (i.e., A. sagrei may be pre-adapted to such habitats before it invaded). Pre-invasion body-size differences may affect the size of prey items these lizards take (Schoener 1967; Roughgarden 1974; but see Floyd & Jenssen 1983). Other possible unquantified niche axes upon which these species may differ in their overlap include differences in insolation and preferred body temperatures. Anolis lineatopus was observed more frequently in the shade than the other two species, and hence may not compete with the other species for shady perches. Cuban and Floridian specimens of A. sagrei are thermophilic and utilize sunny habitats (Ruibal 1961; Salzburg 1984). Preferred body temperatures may differ and prevent overlap among these three species. All of these pre-invasion factors may be involved in facilitating the coexistence that was observed in this Anolis community.

Future studies should involve detailed microhabitat use quantification and account for other niche axes that may help to understand the important ecological and evolutionary factors that are responsible for these faunal assemblages. Such information may be useful in predicting the outcome of invasions on lizard community structure. Finally, it must be stressed that conclusions resulting from this study relative to competitive effects must remain tentative in the absence of data on the entire marked populations over a longer time period, data from controlled field manipulations, and data on the effects of climate, resource availability and the ongoing habitat disturbances upon these species. Such thorough investigations are necessary to reveal post-invasion responses to competitive interactions among these species.

Acknowledgements

We are grateful to Melissa Garretson for assistance with lizard observations and perch height measurements, and also the Hofstra Marine Station officials, including Eugene Kaplan and his staff for making this study possible. We thank George Stevens, Jim Brown and Jim Dixon for constructive comments on the manuscript, and George Stevens, Mark Taper and Lee Fitzgerald for their statistical advice.

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KALLIKREIN-LIKE ENZYME FROM THE VENOM OF
CROTALUS BASILISCUS BASILISCUS
(SERPENTES: CROTALIDAE)

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Midwestern State University, Wichita Falls, Texas 76308

Abstract.—A kallikrein-like enzyme was isolated from the venom of Crotalus basiliscus
basiliscus (Mexican west coast rattlesnake) and assayed for several physiological properties.
Isolation of the enzyme was accomplished with the use of Sephadex G-75, DEAE (diethylaminoethyl) Sephadex A-50, QAE (diethyl [2-hydroxypropyl] aminoethyl) Sephadex A-50 and HPLC Aquapore CX-300 (carboxymethyl) chromatography columns. Fractions were assayed for arginine ester hydrolase activity with the synthetic substrate BAEE (α-N-benzoyl-L-arginine ethyl ester). The purified enzyme exhibited a molecular mass of 31.2 kDa on SDS-PAGE. When added to bovine plasma, the venom enzyme was able to liberate 0.70 moles of bradykinin per mole of enzyme in the isolated rat uterus assay. The venom enzyme, without an exogenous source of kininogen, did not cause an increase in capillary permeability as determined by the Evans blue stain method. The venom enzyme produced a drop of 7 mm Hg in systolic pressure when administered intravenously to a rabbit at 0.07 μg/g body weight.

Recent work has yielded kallikrein-like enzymes from the venoms of Crotalus adamanteus (cf. Markland et al. 1982), Crotalus atrox (cf. Bjarnason et al. 1983), Crotalus ruber ruber (cf. Mori & Sugihara 1988; 1989), Crotalus viridis viridis (cf. Komori et al. 1988), Agkistrodon piscivorus piscivorus (cf. Nikai et al. 1988) and Vipera aspis aspis (cf. Komori & Sugihara 1988). Kallikrein is known to possess arginine ester hydrolase activity and thus is able to cleave the ethyl ester group from the synthetic substrate BAEE (α-N-benzoyl-L-arginine ethyl ester). Many of these enzymes have also been functionally characterized for their kallikrein-like activity (i.e., their ability to release kinins, which cause contraction of visceral smooth muscle, an increase in capillary permeability and hypotension). Physiological assays have been developed to test each of these effects. This study presents findings on the isolation and functional characterization of a kallikrein-like enzyme from the venom of Crotalus basiliscus basiliscus.

Materials and Methods

Whole, lyophilized venom was obtained from Latoxan, lot number PA 346. Chromatography resins, α-N-benzoyl-L-arginine ethyl ester HCl (BAEE), bradykinin, kallikrein, bovine plasma and SDS-PAGE
molecular weight standards were obtained from Sigma Chemical Company. SDS-PAGE pre-made gels were purchased from Bio-Rad. Solvents used for HPLC procedures were of HPLC grade. All other chemicals were of reagent grade quality.

**BAEE activity.**—BAEE activity assays were performed by mixing 5-25 μL of fractionated venom with 3 mL of buffered BAEE substrate (0.1 mg/mL BAEE buffered in a solution of 0.1 M Tris-HCl, pH 8.0 at ambient temperature). Activity was monitored with a Perkin-Elmer Lambda 7 UV/VIS spectrophotometer at 253 nm. BAEE hydrolase units are reported as the change in absorbance per minute per 25 μL of enzyme solution.

**Determination of molecular weight.**—SDS-polyacrylamide gel electrophoresis was carried out on 4-20% gradient and 12% non-gradient polyacrylamide Mini-PROTEAN II ready gels. Electrophoresis buffers, voltages, and coomassie brilliant blue staining and destaining were carried out according to instructions from the manufacturer.

**Kinin-releasing activity.**—The assay method for kinin-releasing activity in the isolated rat uterus was adapted from Erspamer & Erspamer (1962), Trautschold (1970), and Komori et al. (1988). Venom enzyme (5.1 μg/mL) mixed with an equal volume of bovine plasma was tested for the initiation of contractal events for smooth muscle preparations. Uterine horn contractions were monitored on a myograph (Model F-60, Narco Bio-Systems) connected to a pen recorder (Narcotrace 40 physiograph, Narco Bio-Systems) set at a sensitivity of 50 mV/cm.

**Capillary permeability-increasing activity.**—The assay method for capillary permeability-increasing activity was originally described by Miles & Wilhelm (1955) and later modified by Miller & Tu (1989), who used mice. Venom enzyme (2.0 and 2.5 μg in 50 μL), kallikrein (1.2, 2.5 and 25.0 μg in 50 μL) or whole venom (5.2 μg in 50 μL) was injected intradermally using a ½ inch-27 gauge needle.

**Hypotensive activity.**—The procedure for this assay was adapted from Presley (1984:5-8) using the following Locke’s solution (Lockwood 1961): NaCl, 9.0 g; KCl, 0.42 g; CaCl₂, 0.24 g; NaHCO₃, 0.15 g; glucose, 1.0 g/L; pH 7.3 at ambient temperature. Direct carotid blood pressure was measured in the urethane anesthetized New Zealand white rabbit. The carotid catheter was connected to a linear core pressure transducer (Model P-1000B, Narco Bio-Systems) set at 20 mV/cm.
Figure 1. Sephadex G-75 separation of whole venom. Protein absorption at 280 nm (—) was monitored continuously and BAEE hydrolase activity as the change in absorbance at 253 nm/min/mL of fraction (○) was determined as indicated.

Figure 2. DEAE Sephadex A-50 separation of the BAEE hydrolase fraction from the third Sephadex G-75 rechromatography column (not shown). Protein absorption at 280 nm (—) and BAEE hydrolase activity (○) were determined as noted in Fig. 1. KCl concentration, M, (△) was determined by conductivity measurements as indicated.
sensitivity for direct measurement of blood pressure. Heart rate and respiration was monitored through thoracic needle electrodes coupled to a hi-gain coupler and an impedance pneumograph coupler, respectively.

RESULTS

Isolation and molecular weight.—5.050 g of whole venom was dissolved in 45 mL of 50 mM Tris-HCl, 50 mM KCl buffer (pH 7.2 at 0-4° C), and applied to a Sephadex G-75 column (5.5 x 50 cm) equilibrated with the same buffer. A flow rate of 63 mL/hr at 0-4° C was maintained with the use of a peristaltic pump. Fractions were collected every 15 minutes. Fractions B1 (Fig. 1) were pooled, dialyzed, lyophilized and rechromatographed on a second G-75 column equilibrated with a buffer of greater ionic strength (50 mM Tris, 50 mM KCl, 100 mM NH₄Ac, pH 7.2 at 0-4°C). The increase in ionic strength alleviated protein precipitation problems which were observed in the first G-75 column. Fractions containing 59% of the total BAEE hydrolase activity from the second G-75 column were pooled and rechromatographed on a third G-75 column (50 mM Tris-HCl, 50 mM KCl, pH 7.2 at 0-4°C).

Fractions containing 92% of the total BAEE hydrolase activity were applied to a DEAE Sephadex A-50 ion exchange column (2.6 x 81 cm) equilibrated with Tris buffer (50 mM Tris-HCl, 20 mM KCl, pH 7.2 at 0-4° C). The sample was eluted with an isocratic wash of approximately three bed volumes and then developed with a linear salt gradient to 1 M KCl.

Fraction E4 (Fig. 2) was then applied to a QAE Sephadex A-50 ion exchange column (2.6 x 79 cm) equilibrated and developed with buffer and salt gradient identical to the DEAE column.

Aliquots of fraction B5 (Fig. 3) were then applied to an HPLC Aquapore CX-300 cation exchange column (220 x 4.6 mm) equilibrated with 5% buffer A (10 mM Tris-Ac, 0.2 M NH₄Ac, pH 7.0 at ambient temperature) and 95% buffer B (10 mM Tris-Ac, pH 7.0 at ambient temperature). The column was developed with a linear gradient from 5% A to 60% A over 25-40 minutes with a flow rate of 1.0 mL/min and then re-equilibrated with 5% A and 95% B for ten minutes prior to the next run. Fractions B6 (Fig. 4), the kallikrein-like enzyme, were then collected and weighed.

SDS-PAGE of the purified enzyme revealed a single band corresponding to a molecular weight of 31.2 kDa.
Figure 3. QAE Sephadex A-50 separation of the BAEE hydrolase containing fraction 'E4' from the DEAE Sephadex A-50 separation (see Fig. 2). Protein absorption at 280 nm (—), BAEE hydrolase activity (○) and KCl concentration (△) was determined as noted in Fig. 2.

Figure 4. HPLC Aquapore CX-300 chromatographic separation of an aliquote of the BAEE hydrolase containing fraction, B5, from Fig. 3. One of eight runs where protein absorption at 280 nm (—) and BAEE hydrolase activity (○) were determined as noted in Fig. 1 and sodium acetate concentration, M, (△) was calculated from the gradient program.
Table 1. Isolated rat uterus assay (kinin-releasing activity). Assay substances at 110-130 pmol were mixed with an equivolume of bovine plasma (150 μL) unless noted otherwise and incubated at 37° C for five minutes.

<table>
<thead>
<tr>
<th>Assay Mixture</th>
<th>Uterus Contraction (g)</th>
<th>Bradykinine equivalents released (pmol)</th>
<th>Moles of bradykinin released/mole of substance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Enzyme + Plasma</td>
<td>0.75</td>
<td>89</td>
<td>0.70</td>
</tr>
<tr>
<td>Kallikrein* + Plasma</td>
<td>0.93</td>
<td>210</td>
<td>1.9</td>
</tr>
<tr>
<td>Enzyme only</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>Kallikrein only</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>Plasma only</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
</tr>
</tbody>
</table>

* Porcine pancreatic kallikrein; molecular weight = 34 kDa (Fieldler, 1976)

Kinin-releasing activity in isolated rat uterus.—Kinin-releasing activity assays showed that the venom enzyme (3.8 μg, 130 picomoles, in 75 μL), when added to an equal volume of plasma, induced contractions of the isolated rat uterus equal to 0.75 g force (Table 1). Comparison of the bradykinin dose-response curve with the venom enzyme-plasma mixture indicated that the enzyme produced a contraction force equal to the tissue response for 89 pmol of bradykinin. The enzyme, on a per mole basis, released kinin from the plasma corresponding to approximately 0.70 mol of bradykinin.

Capillary-permeability increasing activity.—Intradermal injection of venom enzyme, without an exogenous source of kininogen, did not produce an increase in capillary permeability.

Hypotensive activity.—Intravenous injections of venom enzyme resulted in a small decrease in mean arterial pressure followed by a rapid recovery (Figure 5).

DISCUSSION

The purified enzyme exhibited a molecular mass of 31.2 kDa. Recent studies have shown that other kallikrein-like enzymes from snake venoms have similar masses (Bjarnason et al. 1983; Komori et al. 1988; Mori & Sugihara 1988; Nikai et al. 1988).

The enzyme exhibited the ability to release kinin causing visceral smooth muscle contraction. The equivalent of 0.70 moles of bradykinin released per mole of enzyme indicates a moderate kinin-releasing ability.
Figure 5. Mean arterial pressure of the rabbit receiving venom enzyme. Intravenous injections were given at time 0 (0.07 µg/g body weight) and as indicated by the arrow (0.1 µg/g body weight).

An increase in capillary permeability was not seen following direct intradermal injection of either the venom enzyme or plasma kallikrein. The lack of any capillary permeability response may be due to the lack of sufficient endogenous kininogens in the injection area. Intradermal injections of whole venom did produce a noticeable blue spot of 0.4 cm². The whole venom activity is most likely due to the presence of spreading factors such as hemorrhagic enzymes.

In the preliminary studies, low concentrations of venom enzyme (0.07 µg enzyme per gram of body weight) produced a 7 mm Hg decrease in systolic pressure. Comparisons of this low response to the results obtained with equal concentrations of bradykinin and kallikrein show that the enzyme does not produce a hypotensive kallikrein-like response in the rabbit model. Other kallikrein-like enzymes have been shown to cause sizable decreases in blood pressure resulting in prolonged hypotension in rats (Komori & Sugihara 1988; Komori et al. 1988; Mori & Sugihara 1988). These studies report the results from the administration of kallikrein-like enzymes at considerably higher concentrations than reported in this study. Further studies of the kallikrein-like enzyme concentration effects on blood pressure will be of considerable interest.
ACKNOWLEDGEMENTS

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LITERATURE CITED


ABUNDANCE AND DIVERSITY OF AQUATIC BIRDS ON TWO SOUTH TEXAS OXBOw LAKES

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Abstract.—Avian use of two oxbow lakes located in urban surroundings of south Texas was studied for one year. Both abundance and diversity of aquatic birds were notably reduced in the more intensely developed area. Possible factors resulting in these differences are reviewed.

Recent studies have investigated the relationship between birds and the diversity of habitat in which they are found. MacArthur & MacArthur (1961) reported that foliage height diversity was important for the maintenance of bird species diversity. Rotenberry et al. (1979) noted a positive relationship between vegetational structure and avian diversity. Lancaster & Rees (1979) reported a positive linear relationship between avian diversity and foliage height diversity and an inverse relationship between bird species diversity and the man-made component of structural diversity. Bird species diversity and species abundance have also been shown to decrease with urbanization and to increase with foliage height diversity and total vegetation (Emlen 1974; Guthrie 1974; Lancaster & Rees 1979; Cicero 1980).

In addition to the above studies, many investigators have specifically examined the resulting impact and relationship that man-made changes in the environment have had upon the avian community (Emlen 1974; Gavareski 1976; Rice et al. 1984; Naik & Parasharya 1987; Derleth et al. 1989). This study was undertaken in an effort to determine the nature of man's influence as a factor in determining the use of urban lentic bodies of water by aquatic birds in south Texas.

Study Area

Two oxbow lakes, known locally as resacas, which are located adjacent to the University of Texas at Brownsville campus were selected for observation during the course of this study. The two bodies of water are similar with respect to several physical features. They are less than 200 m apart and separated by a paved roadway and artificially constructed levee. Both are of the same approximate size in surface area (0.1 km$^2$) and lie within 1 km of the Rio Grande and the international
border with Mexico. While similar in many ways, the two bodies of water exhibit differences of major importance.

**Fort Brown Resaca.**—This horse-shoe shaped lake is located in a highly developed urban area. It adjoins the campus of the University of Texas at Brownsville and is surrounded by residential homes, hotels and offices. The grounds in this area are maintained and characterized by the presence of introduced cultivated plants. Lawns are regularly trimmed and there are extensive paved streets and parking areas. While there is occasional weedy vegetation along the shoreline, most of the lake’s edge consists of man-made vertical retaining walls. A nearly constant water level is maintained by the Brownsville Public Utilities Board with water pumped from the Rio Grande. The minimum water depth is maintained near 0.8 m and the bottom is deep silt.

**Lozano Banco.**—This hook-shaped body of water is located in a former agricultural area which is currently in the early stages of succession to streamside woodland and Tamaulipian brushland. The shoreline is heavily vegetated with both native and introduced vegetation including trees and shrubs that form a dense thicket around much of the perimeter. A stand of giant reed grass occupies a small area of the lake margin. While the banks slope naturally around most of the lake, they are very steep adjacent to artificial levees. Lozano Banco receives most of its water from run-off and its level fluctuates. The lake is shallow with a maximum depth of approximately 1 m. The lake bottom slopes gently near the shore and is composed of deep silts.

**Methods**

A bird census of both resacas was conducted on a weekly basis. This consisted of 15 min. walking surveys conducted during midday (Mar. 92 - Feb. 93) and hour-long observational periods conducted at dawn (Aug. 92 - Jan. 93). Observations were also made with binoculars from a vantage point that afforded a view of most of the lake surface and perimeter. Estimates of both numbers of birds and numbers of species were based upon visual observations. Diversity was estimated using Shannon’s formula as given by Begon et al. (1990). While both adult and juvenile birds were included in the estimation of numbers of birds (Figure 1), juvenile birds of uncertain identification were not used in determining the numbers of species (Figure 2) nor the bird species diversity (Figure 3).
Results

During the course of this study 22 species (Table 1) of aquatic birds were recorded present in the study area. Of these, only five species were observed on both bodies of water. These were the Double-crested Cormorant, Neotropic Cormorant, Great Egret, Snowy Egret and Black-bellied Whistling-Duck. The Laughing Gull was observed only on Ft. Brown Resaca. The remaining 16 species were reported only from Lozano Banco.

The total numbers of birds observed during the course of this study (Figure 1) were consistently higher at Lozano Banco than at Fort Brown Resaca. These differences were observed to be greatest during the autumn and early winter months due to the presence of large numbers of migrants. The observed differences during October and November were primarily due to the presence of Cattle Egrets. Additionally, abundance was also affected during these months by the overnight roosting of several species of herons in dense thickets of trees overhanging the water. This was not observed at Fort Brown Resaca.

The number of species, or species richness, was also noted to be consistently higher (Figure 2) at Lozano Banco in all months except May of 1992 when it was equal for both lakes. During that time, only two
species of aquatic birds were observed to be present on each of the two lakes. Diversity (Figure 3) was also equal to or higher at Lozano Banco than that observed at Fort Brown Resaca during most of the year. The most noteworthy exception to this trend was during the period of

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
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<tbody>
<tr>
<td>Podilymbus podiceps</td>
<td>Pied-billed Grebe</td>
</tr>
<tr>
<td>Tachybaptus dominicus</td>
<td>Least Grebe</td>
</tr>
<tr>
<td>Phalacrocorax auritus**</td>
<td>Double-crested Cormorant</td>
</tr>
<tr>
<td>Phalacrocorax brasilianus**</td>
<td>Neotropic Cormorant</td>
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<tr>
<td>Ardea herodias</td>
<td>Great Blue Heron</td>
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<tr>
<td>Bubulcus ibis</td>
<td>Cattle Egret</td>
</tr>
<tr>
<td>Butorides virescens</td>
<td>Green Heron</td>
</tr>
<tr>
<td>Casmerodius albus**</td>
<td>Great Egret</td>
</tr>
<tr>
<td>Egretta caerulea</td>
<td>Little Blue Heron</td>
</tr>
<tr>
<td>Egretta thula**</td>
<td>Snowy Egret</td>
</tr>
<tr>
<td>Egretta tricolor</td>
<td>Tricolored Heron</td>
</tr>
<tr>
<td>Nyctanassa violacea</td>
<td>Yellow-crowned Night-Heron</td>
</tr>
<tr>
<td>Nycticorax nycticorax</td>
<td>Black-crowned Night-Heron</td>
</tr>
<tr>
<td>Anas discors</td>
<td>Blue-winged Teal</td>
</tr>
<tr>
<td>Dendrocygna autumnalis**</td>
<td>Black-bellied Whistling-Duck</td>
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<tr>
<td>Fulica americana</td>
<td>American Coot</td>
</tr>
<tr>
<td>Gallinula chloropus</td>
<td>Common Moorhen</td>
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<tr>
<td>Larus atricilla*</td>
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<td>Sterna maxima</td>
<td>Royal Tern</td>
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<td>Ceryle alcyon</td>
<td>Belted Kingfisher</td>
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<tr>
<td>Ceryle torquata</td>
<td>Ringed Kingfisher</td>
</tr>
<tr>
<td>Chloroceryle americana</td>
<td>Green Kingfisher</td>
</tr>
</tbody>
</table>

*Recorded only on Ft. Brown Resaca
**Recorded on both Ft. Brown Resaca and Lozano Banco
Other species listed were observed only on Lozano Banco

overnight heron roosting. The dominance of these birds appears responsible for this exception.

Discussion

There appears to be a number of man-made factors which could account for or contribute to the differences in numbers of birds, number of species and avian diversity between Fort Brown Resaca and Lozano Banco observed during the course of this study.

Human Activity.—At Fort Brown Resaca, human traffic is continually high; disturbance from pedestrians, vehicular traffic and recreational use from adjacent facilities all appear disruptive of avian activities. This is not the case for Lozano Banco.

Shoreline Vegetation.—The presence of an abundance of both native
and introduced vegetation along and near the shoreline of Lozano Banco appears to represent a major contributing factor in the increased avian activity noted in this area. Likewise, the lack of similar vegetation and its replacement with lawns, paved areas and man-made structures in the Fort Brown area affords little usable vertical habitat adjacent to the shoreline.

Physical Differences.—The nature of the differences in shoreline modification, slope of lake bottom and maintenance of a constant surface water level at Fort Brown Resaca are beyond the scope of this investigation. Likewise are possible differences in bottom sediments and non-avian biota between the two lakes. Additional studies would be required to resolve the effect of these variables upon avian use of the lakes.

Conclusions

This study was conducted upon only two lakes of noted dissimilarity for only one year's duration. Considering this and the number of potential variables involved, the results of this study must be considered preliminary. While it appears likely that the man-made physical and biological changes at Fort Brown Resaca are responsible for the observed reduction in avian abundance and diversity, when compared to Lozano Banco, additional studies are required to substantiate this tentative conclusion. This study should be useful in planning future studies. Meanwhile, the results may provide useful information for those in positions of authority who are responsible for the planning and/or modification of existing bodies of water in urban areas with respect to aquatic bird use.

Acknowledgements

This study was supported in part by funding from the University of Texas at Brownsville. We wish to thank Dana Lee Bohne, Rose Farmer, Mike Farmer, Merriwood Ferguson and Rick Teter for their assistance and to Alfred Richardson, Rodney Sullivan and Alfredo Munoz for reviewing an earlier draft of this paper.

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GENERAL NOTES

FIRST REPORT OF THE ACANTHOCEPHALAN
MACRACANTHORRHYNCHUS INGENS FROM THE DOMESTIC DOG
CANIS FAMILIARIS IN KANSAS

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Dept. of Zoology, Arizona State University, Tempe, Arizona 85287-1501, and
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On 21 August 1993 a single adult specimen of the acanthocephalan Macracanthorhynchus ingens (Oligacanthorhychidae) was collected in Manhattan, Kansas. The 10 cm long female specimen was defecated by a two year old Portuguese water dog which weighed 20 kg and was boarded at a residence located in a wooded hillside area of the city. The specimen of M. ingens was stained in acid carmine, preserved in glycerol, and partially dissected to expose the proboscis for diagnostic purposes. It was distended with ovarian balls at various stages of development. The size and stage of maturity of the specimen is indicative of normal development in the host’s intestine. The specimen is deposited with the United States National Museum (USNM 84482). A follow up fecal examination of the canine host, which receives 136 μg/month ivermectin orally for heartworm prevention, produced only Giardia sp. cysts.

The natural host of M. ingens is the common raccoon Procyon lotor. This animal is an opportunistic omnivore that has a diverse diet which includes insects, frogs, snakes and garbage (Whitney & Underwood 1952; Johnson 1970). Elkins & Nickol (1983) list additional definitive hosts of M. ingens. These include the striped skunk (Mephitis mephitis), mink (Mustela vison) and black bear (Ursus americanus). The domestic dog, Canis familiaris, has also been reported as an occasional definitive host (Fahnestock 1985; Georgi 1992). Beetles assigned to the genera Phyllophaga and Ligyrus (cf. Moore 1946), the millipede Narceus americanus (cf. Crites 1964) and woodroaches of the genus Parcoblatta (cf. Elkins & Nickol 1983) are also reported to represent intermediate hosts. Visceral establishment of M. ingens has been reported in frogs of the genus Rana (cf. Moore 1946) and garter snakes of the genus Thamnophis (cf. Elkins & Nickol 1983). A review of acanthocephalan host systems was presented by Schmidt (1985).
The area of Manhattan, Kansas where this case occurred affords a wide range of insect-amphibian-reptilian host systems with considerable habitat overlap with raccoons and skunks. Woodroaches, millipedes, beetles, and snakes of the genera *Thamnophis* and *Diadophis* are abundant. There are few frogs but the toads *Bufo woodhousei* and *B. cognatus* are common. Raccoons and skunks often enter the grounds of residences in Manhattan during hours of darkness and defecate. Clearly, an enzootic population of *M. ingens* is well established in and around these Manhattan woodlands. The prevalence of *M. ingens* in raccoons in rural Manhattan is 17.4% (Robel et al. 1989)

The canine host is given daily freedom of the grounds and has a history of coprophagy of raccoon feces. This is not, however, regarded as the definitive cause of this reported case. The eggs of *M. ingens* would first have to develop to an infective cystacanth stage in an intermediate insect host. Although unlikely, it is possible that the specimen of *M. ingens* was defecated intact by a raccoon and ingested by the dog. The canine host may also have ingested intermediate or paratenic host(s) which are naturally infected with cystcanths. The means of transmission of *M. ingens* to the canine host remains unclear at this time. Should the intermediate/paratenic hosts prove to be the source of this dog's infection, then *Canis familiaris* should be regarded as a natural host and should be added to the list of regular definitive hosts of *M. ingens*. It is possible that this association has not been commonly observed due to ecological segregation rather than physiological incompatibility. The documentation of an active infection of *M. ingens* in a 10-month-old child in Texas (Dingley & Beaver 1985) attests to the ability of this acanthocephalan species to infect a wider range of vertebrate hosts than previously reported.

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Placobdella parasitica (Rhynchobdellida: Glossiphoniidae) from the Eastern River Cooter (Chelonia: Emydidae) in Oklahoma

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While the large glossiphoniid leech Placobdella parasitica (Say 1824) has been commonly reported throughout much of North America, distributional data on this species from the southern and western states remains poorly known (Sawyer 1972; Klemm 1982). On 15 March 1994, three adult specimens of P. parasitica were collected from the plastron of a single male specimen of the eastern river cooter Pseudemys concinna concinna (LeConte 1830) from Lake Texoma, Marshall County, Oklahoma. The length of the turtle's carapace was 21.5 cm and its width was 15.5 cm. All three leech specimens were dorsoventrally flattened with a greenish-brown dorsum, cream-colored mid-dorsal band of variable width, and irregular lateral patches. The ventrum of each exhibits 8 to 12 bluish-green longitudinal stripes. Specimens measured 2.0 cm, 3.2 cm and 3.5 cm in length. The crop ceca of all three specimens contained blood, indicating a natural association with the turtle. Two specimens (HWML 37846) are
Table 1. Reported turtle hosts of *Placobdella parasitica*.

<table>
<thead>
<tr>
<th>TURTLE SPECIES</th>
<th>REFERENCES</th>
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<tbody>
<tr>
<td><em>Chelydra serpentina serpentina</em></td>
<td>Sawyer 1972, 1986</td>
</tr>
<tr>
<td><em>Chelydra serpentina osceola</em></td>
<td>Ernst &amp; Barbour 1972</td>
</tr>
<tr>
<td><em>Macrolemys temminckii</em></td>
<td>Ernst &amp; Barbour 1972</td>
</tr>
<tr>
<td><em>Sternotherus depressus</em></td>
<td>Dodd 1988</td>
</tr>
<tr>
<td><em>Sternotherus odoratus</em></td>
<td>Ryerson 1915; Sawyer 1972</td>
</tr>
<tr>
<td><em>Kinosternon subrubrum</em></td>
<td>Sawyer &amp; Shelley 1976</td>
</tr>
<tr>
<td><em>Clemmys guttata</em></td>
<td>Ryerson 1915; Sawyer 1972</td>
</tr>
<tr>
<td><em>Clemmys insculpta</em></td>
<td>Koffler et al. 1978; Ricciardi &amp; Lewis 1991</td>
</tr>
<tr>
<td><em>Graptemys geographica</em></td>
<td>Say 1824; Sawyer 1972</td>
</tr>
<tr>
<td><em>Graptemys pseudogeographica</em></td>
<td>Sawyer 1986</td>
</tr>
<tr>
<td><em>Trachemys scripta</em></td>
<td>Martin 1972; Sawyer 1972</td>
</tr>
<tr>
<td><em>Trachemys scripta elegans</em></td>
<td>Hendricks et al. 1971</td>
</tr>
<tr>
<td><em>Pseudemys concinna concinna</em></td>
<td>This study</td>
</tr>
<tr>
<td><em>Pseudemys nelsoni</em></td>
<td>Ernst &amp; Barbour 1972</td>
</tr>
<tr>
<td><em>Chrysemys picta picta</em></td>
<td>Sawyer 1972, 1986</td>
</tr>
<tr>
<td><em>Chrysemys picta marginata</em></td>
<td>Ryerson 1915; Sawyer 1972; Amin 1981; Ricciardi &amp; Lewis 1991</td>
</tr>
<tr>
<td><em>Emydoidea blandingii</em></td>
<td>Sawyer 1972; Amin 1981</td>
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</tbody>
</table>

deposited with the holdings of the H. W. Manter Parasitology Laboratory, University of Nebraska State Museum.

This report of *Placobdella parasitica* represents a new addition to the leech fauna of Oklahoma. It also represents the first record of this species from *Pseudemys concinna concinna*. This leech is commonly reported to blood-feed on *Chelydra serpentina* and *Chrysemys picta* turtles (Sawyer 1972, 1986; Amin 1981), which may represent the preferred hosts for this leech. *Placobdella parasitica* has now been reported from 17 different species and subspecies of turtles (Table 1) as well as *Rana pipens* (cf. Meyer & Moore 1954), indicating that *P.*
parasitica blood-feeds upon a wide variety of turtles and possibly other hosts.

Acknowledgements

The assistance of Dr. John D. Lynch with the turtle identification, the turtle collection by Scott Snyder and the critical reviews of the manuscript by Dr. Duane Hope and Dennis J. Richardson are gratefully appreciated.

Literature Cited


BOOK REVIEW


Although E. A. Kutac and S. C. Caran are listed as authors of this book, five of the eight chapters are actually authored in part or exclusively by others. This is an excellent guide to the natural history of the 19 county area covered in this handbook. The preliminary pages on geological history, climate, ecology and locations of interest are very well done and should serve as a source for professionals as well as for nonprofessionals.

The chapter on birds is well done. The intent of the bird list is to inform about abundance, distribution, and timing of species’ occurrence. It does this well without elaborating on vouching details. Without details on dates of occurrence or other confirming evidence for the status of many species, the list cannot be used as a technical source. But this was not the intent of the authors.

The chapter on mammals represents a useful compilation of mammal species occurring within the defined area of South Central Texas. The scientific names and sequence for species of mammals follows a recent checklist of North American mammals, but no explanation is given for the use of subspecific names for several bats and only species designations for the remainder of the mammals. Although it is unclear how the authors’ determined relative abundance for mammal species, most assessments appear accurate. These minor considerations notwithstanding, the authors have succeeded in elucidating the status of the mammalian fauna within this region of Texas.

The annotated checklist of amphibians and reptiles is a compendium of useful information regarding species abundance, habitat and distribution. There are no errors worth noting and the classification is up to date. The checklist should be useful to both professionals and nonprofessionals. Additionally, there are chapters on fishes, land snails and butterflies of this area of Texas.

Terry C. Maxwell
Robert C. Dowler
Raymond Stone, Jr.
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HELMINTH PARASITES OF UNISEXUAL AND BISEXUAL WHIPTAIL LIZARDS (TEIIDAE) IN NORTH AMERICA.
IX. THE PLATEAU SPOTTED WHIPTAIL (CNEIDIDOPHORUS GULARIS SEPTEMVITTATUS)

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Abstract.—Sixteen percent of 83 specimens of the plateau spotted whiptail lizard, Cnemidophorus gularis septemvittatus Cope 1892, were found to be infected with one or more of six species of parasitic helminths. One percent were found with Oochoristica bivitellobata Loewen 1940, eight percent with tetrathyridia of Mesocestoides sp. Vaillant 1863, one percent with larval Physaloptera sp. Rudolphi 1819, five percent with Parathelandros texanus Specian & Ubelaker 1974, two percent with Pharyngodon warneri Harwood 1932, and six percent with oligacanthorhynchid acanthocephalan cystacanths. This report, the ninth in a series on helminths of the genus Cnemidophorus, reports new host records for Oochoristica bivitellobata, Physaloptera sp., Pharyngodon warneri, and oligacanthorhynchid acanthocephalan cystacanths.

The plateau spotted whiptail, Cnemidophorus gularis (=septemvittatus) septemvittatus Cope 1892, is a large bisexual teiid lizard that ranges from the Big Bend region of Texas south through much of Chihuahua and Coahuila, Mexico (Conant & Collins 1991). This lizard is known from only six counties of southwestern Texas (Dixon 1987; Cordes et al. 1990) where it frequents rocky outcroppings with sparse vegetation in rugged mountainous regions and desert foothills. Little is known about the natural history and ecology of this lizard (Wright & Vitt 1993). Likewise, little has been documented on its parasites. Specian & Ubelaker (1974a; 1974b) described two species of oxyurid nematodes from C. gularis septemvittatus (syn. C. scalaris) in Brewster County, Texas. In addition, McAllister et al. (1991c) reported Mesocestoides sp. tetrathyridia in C. gularis septemvittatus from Presidio County, Texas. To our knowledge, no additional information has been published on parasites of this lizard. The objective of this paper, the ninth in a series of reports on helminth parasites of Cnemidophorus (McAllister 1990a; 1990b; 1990c; 1990d; 1992; McAllister et al. 1991a; 1991b; 1991c), is to provide additional data on the identity, prevalence, and intensity of parasites infecting C. gularis septemvittatus from Texas.
Materials and Methods

Eighty-three juvenile and adult specimens of *C. gularis septemvittatus*, including 44 males and 39 females (mean ± 1 SD for snout-vent length (SVL) = 86.1 ± 16.1, range 47-115 mm) were collected between June to September 1989 and again during May 1990. Most specimens (N = 78) came from "Campo Nuevo" in San Antonio Canyon, 45 km N of Presidio, Presidio Co., Texas (29°53'N, 104°29'W, elevation 900 to 1500 m). The remainder were from sites in Brewster (N = 2), Pecos (N = 1), and Terrell (N = 2) counties. Lizards were killed with .22-caliber rat shot or immobilized with rubber bands and euthanized by overdose with sodium pentobarbital. Lizards were field preserved in 10 percent formalin and stored in 70 percent ethanol until examination. Detailed methods for processing hosts and parasites have been previously described by McAllister (1990a).

Representative helminths have been deposited in the United States National Museum (USNM) Parasite Collection (USDA) Beltsville, Maryland 20705, as follows: *Oochoristica bivitellobata* (USNM 83364), *Mesocestoides* sp. (USNM 83363), *Physaloptera* sp. (USNM 83366), *Parathelandros texanus* (USNM 83367), *Pharyngodon warneri* (USNM 83368), acanthocephalan cystacanths (USNM 83365). Voucher specimens of *C. gularis septemvittatus* are deposited in the University of Arkansas Department of Zoology Collection (UADZ).

Results and Discussion

Thirteen of 83 (16%) specimens of *C. gularis septemvittatus* were found to be infected with at least one kind of helminth (Table 1). Seven specimens (54%) harbored a single parasite whereas multiple infections were observed in six specimens (46%), including two helminths in five lizards and one lizard with three species. Only lizards from Presidio County harbored parasites.

On the average, mature and larger lizards exhibited a higher prevalence of infection as the overall SVL's of infected (102.2 ± 9.4, 84-115 mm, N = 13) and uninfected lizards (83.1 ± 15.2, 47-115 mm, N = 70) were significantly different (Student’s unpaired t-test, t = 6.01, 81 df, P < 0.0005). If juveniles (60.1 ± 8.8, 47-69 mm, N = 13), all of which did not harbor parasites (Table 2), are excluded from the analysis, SVL's of infected and uninfected adults (88.5 ± 10.6, 70-114 mm, N = 57) remain significantly different (t = 4.63, 68 df, P < 0.0005). There was nearly a three-fold difference in prevalence of
Table 1. Helminths found in *Cnemidophorus gularis septemvittatus* from southwestern Texas.

<table>
<thead>
<tr>
<th>Helminth</th>
<th>Site of infection</th>
<th>Prevalence*</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cestoidea</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclophyllidea</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mesocestoides</em> sp.**</td>
<td>coelom, heart, liver, lungs, intestines, mesenteries, ovaries, stomach</td>
<td>7/83 (8%)</td>
</tr>
<tr>
<td><em>Oochoristica bivitellobata</em>**</td>
<td>duodenum</td>
<td>1/83 (1%)</td>
</tr>
<tr>
<td><strong>Nematoda</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spirurida</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Physaloptera</em> sp.***</td>
<td>stomach</td>
<td>1/83 (1%)</td>
</tr>
<tr>
<td>Oxyurida</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Parathelandros texanus</em></td>
<td>rectum</td>
<td>4/83 (5%)</td>
</tr>
<tr>
<td><em>Pharyngodon warneri</em>**</td>
<td>colon, rectum</td>
<td>2/83 (2%)</td>
</tr>
<tr>
<td>Acanthocephala</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oligacanthorhynchida</td>
<td>unidentified cystacanths***</td>
<td>5/83 (6%)</td>
</tr>
</tbody>
</table>

*Number infected/number examined (percent).

**Mesocestoides** sp. tetrathyridia (Cestoidea: Cyclophyllidea) reported previously from 6/70 (9 percent) *C. gularis septemvittatus* by McAllister et al. (1991c).

***New host record.

infection among the sexes as 23 percent of all males and eight percent of all females harbored parasites (Table 2). When SVL’s of these 13 infected lizards are compared, adult male SVL’s (105.9 ± 6.0, 98-115 mm, N = 10) were significantly different (t = 2.96, 11 df, P < 0.005) than SVL’s of adult females (90.0 ± 8.7, 84-100 mm, N = 3). As for within sexual comparisons, SVL’s of infected adult males were significantly different (t = 5.01, 37 df, P < 0.0005) than uninfected adult males (91.8 ± 11.2, 70-114 mm, N = 29) whereas SVL’s of infected adult females were not significantly different (t = 0.924, 29 df, P > 0.20) than SVL’s of uninfected adult females (85.1 ± 9.0, 70-106 mm, N = 28).

Three third-stage larval spirurid nematodes, *Physaloptera* sp. Rudolphi 1819, were found in a single male whiptail (UADZ 3967, SVL = 111 mm) collected in May 1990. Although prevalence of infection and intensities may be low in some whiptails, as is the case here, these
Table 2. Prevalence of helminths infecting different age, sex, and size classes of *C. gularis septemvittatus* from southwestern Texas.

<table>
<thead>
<tr>
<th>Age, sex, and size class*</th>
<th>Prevalence**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juveniles (47-68 mm SVL)</td>
<td>0/13 (0%)</td>
</tr>
<tr>
<td>Adult females (70-106 mm SVL)</td>
<td>3/31 (10%)</td>
</tr>
<tr>
<td>Adult males (70-115 mm SVL)</td>
<td>10/39 (26%)</td>
</tr>
<tr>
<td>All females (47-106 mm SVL)</td>
<td>3/38 (8%)</td>
</tr>
<tr>
<td>All males (52-115 mm SVL)</td>
<td>10/45 (22%)</td>
</tr>
<tr>
<td>All adults (70-115 mm SVL)</td>
<td>13/70 (19%)</td>
</tr>
<tr>
<td>All lizards (47-115 mm SVL)</td>
<td>13/83 (16%)</td>
</tr>
</tbody>
</table>

*Lizards that reached SVL’s ≥ 70 mm were considered sexually mature.

**Number infected/number examined (percent).

spirurids have been reported numerous times from *Cnemidophorus* spp. (cf. McAllister et al. 1992).

Ten oxyurid nematodes, *Pharyngodon warneri* Harwood 1932, each were found in two adult male *C. gularis septemvittatus* (UADZ 3636, 3766, SVL = 99, 105 mm) collected in June 1989 and May 1990. This nematode is a common component of the helminth fauna of whiptail lizards (McAllister 1990d, 1991a).

Two linstowiid tapeworms, *Oochoristica bivitellobata* Loewen 1940, were found in a male *C. gularis septemvittatus* (UADZ 3625, SVL = 100 mm) collected in June 1989. This cestode is another common parasite of *Cnemidophorus* spp., although prevalence of infection may be quite low (McAllister et al. 1991b).

Six oxyurid nematodes, *Parathelandros texanus* Specian & Ubelaker 1974, were found in four (three males, one female) *C. gularis septemvittatus* (UADZ 3625, 3634, 3646, 3658, SVL = 99.0 ± 10.4, range 84-107 mm) collected in June and July 1989; mean intensity was 1.5 ± 0.6 worms. The type locality of *P. texanus* is in nearby Brewster County (Specian & Ubelaker 1974a), approximately 150 km southeast of the present locale in Presidio County. Specian & Ubelaker (1974a) previously reported *P. texanus* from *C. gularis septemvittatus* (syn. *C. scalaris*). It has also been reported from three of 58 (5%) *C. dixoni* at the Campo Nuevo site (McAllister et al. 1991a) as well as three of 27 (11%) *C. tesselatus* from Presidio County, Texas (McAllister 1990a),
one of 289 (0.3%) *C. gularis* from Jeff Davis County, Texas (McAllister 1990d), and one of 23 (4%) *C. flagellicaudus* from Catron County, New Mexico (McAllister 1992). Other hosts and localities include *C. inornatus*, *C. tigris* (=*marmoratus*), *Sceloporus merriami*, *S. undulatus*, *Cophosaurus texanus*, and *Urosaurus ornatus* from Presidio County, Texas (Specian & Ubelaker 1974a), and *U. ornatus* from Arizona (Babero & Matthias 1967; Walker & Matthias 1973).

Oligacanthorynchid acanthocephalan cystacanths were recovered from five male *C. gularis septemvittatus* (SVL = 107.8 ± 7.7, range 99-115 mm) collected in June 1989 and May 1990. Cystacanths are apparently common helminths of whiptails as they have been reported previously from *Cnemidophorus* spp., including *C. dixoni* from the same site included herein (McAllister et al. 1991a).

In summary, four new host records are documented for parasites of *C. gularis septemvittatus*, and all of its parasites are shared with the unisexual species, *C. dixoni* A and *C. tesselatus*. This is not surprising given that *C. gularis septemvittatus* is considered to be one of the parental congener of both species by Wright & Vitt (1993).

Acknowledgments

We wish to thank A. Real, general manager of the Mesquite Ranch, Presidio County, Texas, for lodging and field assistance for JEC. Lizard collections were made under the authority of Texas Parks and Wildlife Department Scientific Collecting Permit no. 61.

Literature Cited


checkered whiptail (*Cnemidophorus tesselatus*). J. Wildlife Dis., 26:139-142.


CRANIAL AND DENTAL VARIATION IN THE NINE-BANDED ARMADILLO, Dasyus novemcinctus, FROM TEXAS AND OKLAHOMA

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

Abstract.—Variations of cranial and dental features were examined in the skulls of 60 specimens of Dasyus novemcinctus from north Texas and southern Oklahoma. Each specimen was assigned to one of three relative age groups (subadult, adult or old adult) based on the degree of fusion of ventral braincase elements. Measurements of cranial and mandibular characters were quantitatively analyzed. Evidence for sexual dimorphism appears lacking. The considerable size overlaps of morphometric measurements between relative age groups suggests a rapid and perhaps less-than-uniform rate of growth among individuals. Timing and sequence of tooth eruption, tooth loss, and dental anomalies are also described.

The nine-banded armadillo (Dasyus novemcinctus) is a common and conspicuous mammal across much of its range. While much has been written about the general anatomy, physiology, and reproductive biology of this species (for summaries refer to Newman & Patterson 1910; Newman 1913; Talmage & Buchanan 1954; McBee & Baker 1982), few efforts have been directed towards the investigation of morphological variation within this species. No comprehensive assessment of geographic variation exists for this species, although the topic has received cursory treatment in studies of broader taxonomic scope (Wetzel & Mondolfi 1979; Wetzel 1985). This includes such aspects as cranial and dental variation, growth and development, and of tooth replacement. Post-partum growth and development have yet to be detailed, although details of embryonic and fetal stages of development have long been known (e.g. Newman 1913; Martin 1916). An understanding of these aspects of armadillo biology remains in need of clarification.

Detailed studies of nongeographic variation do not exist, although regional comprehensive treatments of mammals often provide representative measurements such as those by Lowery (1974) for Louisiana, Bee et al. (1981) for Kansas, Schmidly (1983) for east Texas, Dalquest & Horner (1984) for north Texas and Sealdander & Heidt (1990) for Arkansas. Perhaps a reason for this void in the literature on such a widespread, conspicuous, and regionally common mammal is due to its
Figure 1. Cranial and mandibular measurements of *Dasypus novemcinctus* utilized in this study and summarized in Table 1. Abbreviations and characters are as follows: sk, greatest length of skull; na, greatest width of nasals; ro, rostral width; zy, greatest zygomatic width; io, interorbital breadth; pm, length of premaxillary; mx, length of maxillary, pa, length of palatine; oc, occipital breadth; ut, length of maxillary (upper) tooth row; lt, length of mandibular (lower) toothrow.

poor representation in many systematic collections. This observation is supported by the surprisingly few specimens reported from regions such as Louisiana (N=73; Lowery 1974) and east Texas (N=49; Schmidly 1983), where the armadillo is particularly abundant. This may be because most existing study specimens of *D. novemcinctus* are obtained by salvage of dead animals from along roadways and such collections are often considered an inconvenient or unpleasant task to perform.

A series of skulls of *D. novemcinctus* from Texas and southern Oklahoma comprise the basis for this examination of variation by individual, sex, and age in this species. A method of determining relative age groups within the species is described, which may encourage investigations of geographic patterns of cranial variation in the nine-banded armadillo.

Methods and Materials

Eleven measurements were attempted from the skulls and mandibles of 60 specimens of *Dasypus novemcinctus* originating from Texas and
Figure 2. Ventral view of braincase in a subadult *Dasypus novemcinctus*, as indicated by open sutures (arrows). Components are: ps, presphenoid; bs, basisphenoid; and bo, basioccipital.

southern Oklahoma (Appendix 1). These included right alveolar toothrows of the mandible and maxillary, greatest skull length, greatest zygomatic breadth, least interorbital breadth, greatest width of nasals, basal width of rostrum, greatest occipital breadth, and greatest lengths of the premaxillary, maxillary, and palatine bones from along the medial suture as viewed from the ventral perspective (Figure 1). Measurements were taken with a digital caliper, and recorded to the nearest 0.01 mm, although the fragmentary or damaged nature of some material prevented obtaining all measurements from many specimens.

Dental observations on tooth eruption patterns and congenital anomalies were recorded for each specimen. Tooth losses considered as natural events were distinguished from accidental loss during the preparatory process by the partial or complete filling in of alveoli by spongy bone.

When possible, specimens were classed by sex. Three age classes were assigned on the basis of ventral braincase suture closures between the basioccipital and basisphenoid, and between the basisphenoid and presphenoid (Figure 2). Subadults were defined by the persistence of both sutures. Young adults were characterized by fusion of the basioccipital with basisphenoid, and fully erupted permanent dentition. Specimens defined as old adults were those in which both braincase sutures were obliterated.

Each month of the year was represented, except for the period of
Table 1. Variation by age class in cranial measurements (in mm) of *Dasypus novemcinctus* from the Rolling Plains of Texas and Oklahoma. Descriptive statistics are: sample size (N), mean, standard deviation (SD), range, and coefficient of variation (CV).

<table>
<thead>
<tr>
<th>Age Class</th>
<th>(N)</th>
<th>Mean +SD</th>
<th>Range</th>
<th>CV</th>
<th>Duncan's</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subadult</td>
<td>(19)</td>
<td>95.34 + 3.29</td>
<td>86.10 - 100.59</td>
<td>3.45</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(14)</td>
<td>101.01 + 1.80</td>
<td>97.07 - 104.17</td>
<td>1.79</td>
<td></td>
</tr>
<tr>
<td>Old adult</td>
<td>(15)</td>
<td>102.37 + 2.27</td>
<td>99.09 - 107.26</td>
<td>2.21</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(21)</td>
<td>16.83 + 2.84</td>
<td>11.31 - 23.28</td>
<td>16.89</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(17)</td>
<td>18.63 + 2.12</td>
<td>14.92 - 23.03</td>
<td>11.39</td>
<td></td>
</tr>
<tr>
<td>Old adult</td>
<td>(19)</td>
<td>19.12 + 1.49</td>
<td>16.94 - 21.88</td>
<td>7.80</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(23)</td>
<td>22.23 + 0.91</td>
<td>21.37 - 24.78</td>
<td>3.91</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(17)</td>
<td>24.34 + 0.95</td>
<td>22.98 - 26.10</td>
<td>3.89</td>
<td></td>
</tr>
<tr>
<td>Old adult</td>
<td>(20)</td>
<td>24.56 + 0.84</td>
<td>22.64 - 25.91</td>
<td>3.43</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(14)</td>
<td>38.02 + 1.79</td>
<td>35.18 - 40.41</td>
<td>4.70</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(12)</td>
<td>40.91 + 1.82</td>
<td>38.21 - 43.79</td>
<td>4.44</td>
<td></td>
</tr>
<tr>
<td>Old adult</td>
<td>(12)</td>
<td>42.09 + 1.86</td>
<td>38.83 - 45.10</td>
<td>4.42</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(16)</td>
<td>9.42 + 0.65</td>
<td>8.14 - 10.18</td>
<td>6.90</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(16)</td>
<td>10.15 + 0.48</td>
<td>9.31 - 11.12</td>
<td>4.69</td>
<td></td>
</tr>
<tr>
<td>Old adult</td>
<td>(12)</td>
<td>10.29 + 0.54</td>
<td>9.32 - 11.04</td>
<td>5.27</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(19)</td>
<td>23.55 + 0.72</td>
<td>21.72 - 24.84</td>
<td>3.04</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(16)</td>
<td>23.92 + 0.79</td>
<td>22.10 - 25.10</td>
<td>3.31</td>
<td></td>
</tr>
<tr>
<td>Old adult</td>
<td>(21)</td>
<td>24.54 + 0.92</td>
<td>22.76 - 26.60</td>
<td>3.75</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(16)</td>
<td>8.56 + 0.97</td>
<td>7.21 - 10.57</td>
<td>11.36</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(16)</td>
<td>9.05 + 0.82</td>
<td>7.53 - 10.36</td>
<td>9.04</td>
<td>N.S.</td>
</tr>
<tr>
<td>Old adult</td>
<td>(13)</td>
<td>8.79 + 0.50</td>
<td>7.92 - 9.92</td>
<td>5.71</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(23)</td>
<td>37.14 + 2.31</td>
<td>32.20 - 41.17</td>
<td>6.23</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(17)</td>
<td>39.52 + 1.47</td>
<td>36.17 - 41.63</td>
<td>3.73</td>
<td></td>
</tr>
<tr>
<td>Old adult</td>
<td>(19)</td>
<td>39.45 + 1.70</td>
<td>39.45 - 43.17</td>
<td>4.31</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(23)</td>
<td>16.98 + 1.32</td>
<td>14.61 - 19.17</td>
<td>7.79</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(17)</td>
<td>18.29 + 2.03</td>
<td>11.95 - 20.70</td>
<td>11.10</td>
<td></td>
</tr>
<tr>
<td>Old Adult</td>
<td>(20)</td>
<td>19.23 + 1.01</td>
<td>17.44 - 20.79</td>
<td>5.26</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(22)</td>
<td>25.19 + 1.39</td>
<td>20.80 - 27.43</td>
<td>5.53</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(17)</td>
<td>25.64 + 1.29</td>
<td>22.74 - 28.16</td>
<td>5.03</td>
<td>N.S.</td>
</tr>
<tr>
<td>Old adult</td>
<td>(19)</td>
<td>25.85 + 1.69</td>
<td>21.57 - 28.28</td>
<td>6.54</td>
<td></td>
</tr>
<tr>
<td>Subadult</td>
<td>(22)</td>
<td>25.54 + 1.56</td>
<td>22.34 - 28.89</td>
<td>6.12</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>(17)</td>
<td>26.88 + 1.02</td>
<td>25.54 - 29.18</td>
<td>3.80</td>
<td></td>
</tr>
<tr>
<td>Old adult</td>
<td>(20)</td>
<td>26.75 + 0.89</td>
<td>25.06 - 29.12</td>
<td>3.31</td>
<td></td>
</tr>
</tbody>
</table>

1. One-way analysis of variance (ANOVA): **=0.01 >P>0.001.

2. Duncan's Multiple Range Test. Age classes grouped together are not significantly different (P<0.05).
June-September, during which time a single animal was recorded from 5 July. All examined specimens are deposited in the Midwestern State University (MWSU) Collection of Recent Mammals.

Statistical analyses were performed with the Number Cruncher Statistical Systems (NCSS; Hintze 1990). Two-way ANOVAs (by sex and age) were conducted to assess the interactive effects between sex and age for each measurement, and found to be negligible. Sexual dimorphism was then evaluated with one-way ANOVAs by age class for each character. Only subadults displayed any variation by sex, and these differences (palatine length, $P=0.0435$; interorbital breadth, $P=0.0491$) were marginally significant. Therefore, individuals of both sexes were pooled with unsexed individuals for one-way ANOVAs to evaluate age variation for each character. Significant subsets of age groupings for each set of measurements were determined by Duncan’s multiple range tests.

Results and Discussion

Relative age determinations.—A fairly accurate means of assigning individuals from natural populations to relative age categories is a necessary prerequisite to any meaningful study of morphological variation in *Dasypus novemcinctus*, for which no hard data exists in the literature on postpartum growth and development of the species.

Skeletal and dental observations lend support to the validity of our relative age groupings based on crania, although considerable overlap exists among each age group for all measurements (Table 1). Four of the 23 subadult individuals (as defined by cranial fusions) still retained their deciduous dentition, 15 were marked by newly erupting permanent dentition (e.g. Figure 3), and the remaining seven had new to lightly
worn permanent dentition. Each of the seven skeletons from animals of this age category were characterized by persistent epiphyseal cartilage.

No skeletons were available from animals designated as young adults, although each skull from this age category possessed fully emerged and unworn or little worn permanent dentition. Dentition of old adults was typically worn, and tooth loss was prevalent. Of the six skeletons of older animals available for inspection, all epiphyseal sutures were fused beyond recognition. Additionally, while we do not have reproductive data for all specimens, each animal for which we have data inferring reproductive maturity (males with enlarged testes and lactating or pregnant females) had been classed as old adults.

If Martin (1916) is correct in her assessment that animals achieve near-adult size within four to six months, then most specimens designated as subadults are less than one year old. The chronological distribution of subadults in our study was continuous October-April, with peaks in April (N=7) and November (N=4), doubtless reflecting the extended six-month breeding season and year-around occurrence of juvenile specimens (< 3 kg) as reported by McDonough (1990). The young adult stage probably represents individuals in their second year, and the range of ages for animals classed as old adults may span many years, for Crandall (1974) provides the longevity for a zoo animal at more than six years, and McDonough (1994) refers to a captive specimen exceeding 22 years old.

Morphometric variation.—Significant age variation exists for all characters but premaxillary length. However, extensive overlaps in size occur for each of the 11 measurements. The arbitrary nature of age category assignments doubtless contributes to this observation, and individual rates of age-diagnostic cranial fusions cannot be discounted.

Subadults were significantly smaller than older age categories for eight of the characters examined, although only two characters distinguished young adults from older individuals. Morphometric similarity of the two older relative ages suggests that the rapid growth rates postulated by Martin (1916) decelerate during the second year, followed by an imperceptible rate of growth for the duration of the life of an individual.

Dentition—Martin’s (1916) examination of a large series of embryos and newborn specimens provided a detailed assessment of the early dental development and typical dental formula of *D. novemcinctus*. 
Based on her account, young animals are born with eight functional upper teeth which originate on the maxillary. Only the first seven are apparently replaced by permanent teeth. The last eight of 13-14 tooth germs in the lower jaw ultimately give rise to milk teeth, although only the first seven of these are replaced by permanent teeth.

This study substantiates Martin’s (1916) description of the typical functional armadillo dentition as comprised of eight teeth in each of the upper and lower quadrants, and that the last of each tooth row lacks a deciduous precursor. She asserted that premolars, canines, and incisors were probably represented among the deciduous and replacement teeth. This cannot apply to upper teeth, which all originate in the maxillary, for when present in therian mammals, incisors occur on the premaxillary and the canine at the premaxillary-maxillary junction. While we agree that the posteriormost teeth of both upper and lower dental batteries are molars, precise homologies of the other teeth cannot be made with any certainty. As a matter of expedience in numbering the teeth, we refer to deciduous teeth and their replacements as premolars, and to the last single tooth in each tooth row as a molar.

Deviation from the normal 8/8 dental formula in *D. novemcinctus* attributed to tooth loss appears to be a function of age, and presumably is not particularly detrimental for a species that feeds mostly on soft-bodies invertebrates. Loss of the simple, peg-like teeth of armadillos during the cleaning of cranial materials is common, and leaves a well-defined alveolus, and unless only recently lost, the alveoli of teeth lost during the life of an animal are initially filled in with a scaffolding similar in appearance to spongy, or perhaps woven, bone. Ten of 26 subadults were missing teeth, as well as seven of 16 young adults, and 14 of 20 old adults. The upper molars were most commonly missing, and contributed to most instances of tooth loss among the subadults. One cannot discount the possibility that these small molars sometimes never erupt, for there was seldom any trace of spongy or cancellous bone which fills empty the empty alveolus of teeth lost during life. Among specimens of the two younger age classes, only one individual (MWSU 19514) was missing a permanent upper premolar. Among old adults, eight specimens were missing one or more permanent premolars, and two particularly aged individuals (MWSU 1729 and 19215) were lacking a total of 6 and 12 premolars from their dentition.

Tooth replacement of premolars occurs in subadults nearly the size of adults. However, specimens varying in size and exhibiting comparable stages of tooth replacement were taken in every month but March-
September, suggesting either a prolonged replacement process or considerable variation in timing of the acquisition of adult dentition.

The upper molars are typically erupted prior to full emergence of their lower counterparts. However, eruption sequences of upper and lower premolars appear to be almost simultaneous events, initiated by the appearance of the fourth, fifth, and sixth premolars (Figure 3). Martin (1916) first noted that the permanent teeth often wear through the deciduous teeth, leaving persistent remnants along the anterior and posterior margins of the alveoli. We found such traces to be common in armadillos of all ages, and even the largest and possibly oldest of examined specimens (MWSU 19542; as determined by greatest skull length and extent of tooth wear and loss) still retained traces of nine deciduous teeth along the alveolar margins.

Dental variation attributed to developmental or genetic factors was noted in four specimens. A very small supernumerary tooth, little more than a slender spicule and likely derived from one of the usually atrophied anterior tooth buds noted by Martin (1916), marked the lower left jaw of one animal (MWSU 19515), just anterior to the normal dentition. The maxillary tooth rows of another animal (MWSU 1681), although comparable in length and normal in tooth composition, were staggered, with the left row situated anteriorly by about 10 mm. A third specimen (MWSU 18214) possessed five sets of paired maxillary teeth and one set of paired mandibular teeth (Figure 4a), apparently the result of a splitting of the tooth buds. The fourth aberration (MWSU 19215) involved the staggered clustering of three premolars on the left maxillary toothrow and of two teeth on the right (Figure 4b).

**Additional Investigations**

Despite the fact that *Dasypus novemcinctus* is both common and conspicuous throughout much of its range, detailed studies of geographic variation in this species are lacking. Of particular interest would be comparisons between populations originating from animals introduced into Florida, which have since spread and made contact with those of the original range. This study suggests that both sexed and unsexed specimens can be pooled for such analyses, although efforts to collect or salvage additional specimens will probably be necessary to bolster sample sizes in many areas.

Published information on early life history of the nine-banded armadillo from neonate through juvenile stages is both sketchy and
Figure 4. Aberrant alveolar placement in upper dentition of two old adult *Dasypus novemcinctus*: a) "twinning" of teeth (MWSU 18214); and b) alveolar gathering (MWSU 18215). Stippling indicates alveolus filled with spongy bone, following tooth loss earlier in life.

anecdotal. Postpartum development and growth rates with known-aged individuals have yet to be detailed in the literature, and such data may be useful in assigning absolute ages to museum specimens and to test the accuracy of our relative age groupings.

Acknowledgments

We wish to thank the two anonymous reviewers whose thoughtful comments and suggestions on an earlier version of this manuscript greatly improved the final product.

Literature Cited


Appendix

Following is a listing of localities and MWSU numbers for 60 specimens of *Dasypus novemcinctus* from the Midwestern State University Collection of Recent Mammals examined during this study. Counties are listed in alphabetic order by state.

**Oklahoma.**—Greer County: 7.5 mi W of Quartz Mountains State Park, one specimen (16267). Jackson County: 8 mi E of Altus, one specimen (13342). Roger Mills County: 1 mi S of Cheyenne, one specimen (16630). Stephens County: 8 mi N, 5 mi W of Waurika, one specimen (16360).

**Texas.**—Archer County: Lake Kickapoo, one specimen (9961); 2 mi N of Scotland, one specimen (18453); Archer City, two specimens (1683 & 11173). Baylor County: 8 mi NE of Seymour, one specimen (6422); 7.3 mi E of Seymour, one specimen (19516). Clay County: no specific locality, one specimen (1198); 3 mi N of Shannon, one specimen (17105); 15 mi N of Henrietta, one specimen (15442); 4.2 mi N of Henrietta, one specimen (19515); 7 mi W of Henrietta, one specimen (13378); 4 mi W of Henrietta, one specimen (17103). Cooke County: 5 mi E of Saint Jo, one specimen (7512). Grayson Co.: 5 mi N of Gordonville, one specimen (19213). Hopkins County: 10 mi N of Sulphur Springs, one specimen (16706). Jack County: 5 mi W of Crafton, four specimens (1759-1762); 36 mi S of Wichita Falls, one specimen (1682); 7.4 mi N of Graford, one specimen (18722); 15 mi N, 2 mi W of Jacksboro, one specimen (11525); 14 mi N, 1 mi W of Jacksboro, one specimen (13377). Montague County: 6 mi NNE of Nocona, one specimen (16705); 4.7 mi NW of Nocona, one specimen (18491); 5.6 mi W of Nocona, one specimen (19542); 3 mi E of Nocona, one specimen (19970); 3 mi E of Forestburg, one specimen (10983); 3 mi S of Vashti, one specimen (11204). Stephens County: 18 mi N of Breckenridge, one specimen (19513); 15 mi NE of Breckenridge, one specimen (3130). Wichita County: no specific locality, two specimens (1199 & 11175); 2.7 mi ENE of Kamay, one specimen (18137); 3 mi N of Iowa Park, one specimen (11174); 1 mi S of Iowa Park, one specimen (15441); near Iowa Park, one specimen (19517); 6 mi NE of Punkin Center, one specimen (19215); 10 mi S of Electra, one specimen (19512); 10 mi S of Burk Burnett, one specimen (13379); 10 mi W of Wichita Falls, one specimen (18214); 2 mi W of Wichita Falls, one specimen (15440); Wichita Falls, 10 specimens (1201, 1274, 1465,
1729, 7208, 10984, 17046, 19214, 19514 & 19518). Wise County: no specific locality, one specimen (1681). Young County: 1.3 mi S of Markley, one specimen (18721); 3 mi W, 3.8 mi S of Graham, one specimen (17104); 14 mi S of Windthorst, one specimen (16704).
DISTRIBUTIONAL RECORDS OF SMALL MAMMALS FROM THE SOUTHWESTERN ROLLING PLAINS OF TEXAS

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Abstract.—Distributional notes based upon recent field collections are reported for nine species of small mammals from the southwestern Rolling Plains of Texas. These include one mole (Scalopus), one bat (Tadarida), one armadillo (Dasypus), one kangaroo rat (Dipodomys), two woodrats (Neotoma) and three mice (Reithrodontomys and Baiomys).

Recent field studies conducted on the southwestern Rolling Plains of Texas have resulted in the collection of specimens of nine mammalian species, which represent county records or additional distributional data for these species from this area of the state. The following species accounts are the result of this research. Voucher specimens are deposited with the holdings of The Museum at Texas Tech University (TTU).

Scalopus aquaticus aereus (Bangs)
(Eastern Mole)

*Distributional notes.*—A single specimen of the eastern mole was collected south of White River Lake in Garza County. The nearest reported occurrence of *S. aquaticus aereus* is from Dickens County, approximately 40 km to the northeast (Choate 1990). This record of the eastern mole represents the first from the escarpment breaks of the Rolling Plains in Garza County.

*Material examined.*—12 mi S of White River Lake, Garza County, Texas, 6 December 1982, one specimen (TTU 40657).

*Habitat.*—Soils at the collection locality are loamy, fine sands, which are suitable for habitation by moles.

Tadarida brasiliensis mexicana (Saussure)
(Brazilian Free-tailed Bat)

*Distributional notes.*—Although this species is distributed statewide in Texas (Hall 1981), records are most common from the central and Trans-Pecos regions of Texas (Schmidly 1977; Manning et al. 1987).
Schmidly (1991) lists this species from adjacent Garza and Stonewall counties. This is the first report of specimens from Kent County.

**Material examined.**—Girard, Kent County, Texas, 9 October 1984, 24 specimens (TTU 41952-41965, 41967-41974, 49285-49286); 17 October 1985, 62 specimens (TTU 43205-43206, 45461-45520); 23 September 1986, six specimens (TTU 49279-49284). Specimens include fluid-preserved, skins and skulls, and skeletons.

*Dasypus novemcinctus mexicanus* Peters
(Nine-banded Armadillo)

**Distributional notes.**—Although the armadillo ranges throughout eastern and southern Texas (Schmidly 1983) and is currently expanding its range onto the Llano Estacado (Jones et al. 1993), there are few records of occurrence for the southwestern Rolling Plains. A single specimen each for both Scurry and Garza counties represent new county records for this species.

**Material examined.**—12 mi N, 9 mi W of Snyder, Scurry County, Texas, 6 June 1993, one specimen (TTU 63409). 8 mi S, 9 mi E. of Post, Garza County, Texas, 22 July 1993, one specimen (TTU 63408).

*Dipodomys ordii medius* Setzer
(Ord’s Kangaroo Rat)

**Distributional notes.**—This species has been reported to occur throughout west-central Texas (Hollander et al. 1987) and has been taken in several counties of the Rolling Plains region (Jones et al. 1991). This report represents the first specimen record for Kent County.

**Material examined.**—7 mi S, 17 mi W of Clairemont, Kent County, Texas, 20 November 1993, three specimens (TTU 63393-63395). One female specimen (TTU 63394) was gravid with three fetuses measuring 19mm in crown-rump length.

**Habitat.**—Specimens were collected along the sandy terraces of the Double Mountain Fork of the Brazos River southwest of Clairemont.

*Reithrodontomys megalotis megalotis* (Baird)
(Western Harvest Mouse)

**Distributional notes.**—The western harvest mouse exhibits a widespread distribution on the Llano Estacado and ranges southward into the
Trans-Pecos region of Texas (Davis & Schmidly 1994). This species was previously believed to be restricted to the Llano Estacado at the extreme southeastern part of its range (Choate et al. 1992). This report extends the range of this species onto the western Rolling Plains.

Material examined.—7 mi S, 17 mi W of Clairemont, Kent County, Texas, 3 April 1993, one specimen (TTU 63054). 3 mi N, 9 mi E of Justiceburg, Garza County, Texas, 1 May 1993, one specimen (TTU 63315).

Habitat.—The collection locality southwest of Clairemont is adjacent to the Double Mountain Fork of the Brazos River in an area of sandy, alluvial soil. Vegetation was dense and dominated by tall grasses. The collection locality northeast of Justiceburg is in an area of upland mesquite rangeland.

Reithrodontomys montanus griseus Bailey
(Plains Harvest Mouse)

Distributional notes.—The plains harvest mouse is found in western and central Texas (Davis & Schmidly 1994). This report represents the first record of this species from Kent County. This species appears to prefer more xeric, upland habitats than does R. megalotis (cf. Jones et al. 1983). Although these two species of harvest mice are sympatric in parts of their ranges in Texas, they are usually separated in their specific habitats and are rarely taken together at the same locality.

Material examined.—7 mi S, 17 mi W of Clairemont, Kent County, Texas, 3 April 1993, two specimens (TTU 63057-63058); 20 November 1993, one specimen (TTU 63396). All three specimens are males with testicular measurements of 5 by 3 mm for the April specimens and 2 by 1 mm for the November specimen.

Baiomys taylori taylori (Thomas)
(Pygmy Mouse)

Distributional notes.—The expansion of the geographic range of the pygmy mouse to include the Llano Estacado and adjacent areas was summarized by Choate et al. (1990). This species is distributed over the eastern two-thirds of the state wherever suitable habitat may be found, but records from the southwestern Rolling Plains previously were lacking.

Material examined.—7 mi S, 17 mi W of Clairemont, Kent County,
Texas, 3 April 1993, three specimens (TTU 63039-63041); 24 June 1993, one specimen (TTU 63331). A single specimen (TTU 63331) was gravid with three fetuses measuring 5 mm in crown-rump length.

**Habitat.**—The habitat at this locality consists of sandy alluvial terraces dominated by sand dropseed (*Sporobolus cryptandrus*) and other tallgrass species.

*Neotoma albigula albigula* Hartley  
(White-throated Woodrat)

**Distributional notes.**—The white-throated woodrat is distributed throughout much of northwestern, central, and Trans-Pecos Texas (Jones & Jones 1992), but records from the southwestern Rolling Plains are rare. This report represents the first record of this species from Kent County.

**Material examined.**—7 mi S, 17 mi W of Clairemont, Kent County, Texas, 12 May 1993 and 20 November 1993, four specimens (TTU 63340-63342, 63404).

**Habitat.**—This species prefers saxicolous habitats. The collection locality in Kent County is in the rocky, juniper woodlands of the escarpment breaks.

*Neotoma micropus canescens* J. A. Allen  
(Southern Plains Woodrat)

**Distributional notes.**—The southern plains woodrat is found in the western two-thirds of Texas (Jones & Jones 1992), though no previous records from Kent County exist.

**Material examined.**—7 mi S, 17 mi W of Clairemont, Kent County, Texas, 3 April 1993, one specimen (TTU 63059); 12 May 1993, one specimen (TTU 63345). One specimen (TTU 63059) was gravid with two fetuses measuring 10 mm in crown-rump length.

**Habitat.**—Specimens were collected in an area of sandy, alluvial soils dominated by wild plum (*Prunus* sp.).

**Acknowledgments**

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HYDROCARBON DEGRADING BACTERIA
AT OIL SPRINGS, TEXAS

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Abstract.—Hydrocarbon degrading bacteria capable of heterotrophic growth in air were isolated from the oily mousse (biodegraded oil) from two separate sites at Oil Springs in east Texas. This is an area of long-standing crude oil seepage into a freshwater system. Of the four species of bacteria isolated from one site, and the five from the other, only two species were common to the oil at both sites. The isolates of these common species, however, were biotypically different from each other. Samples from both sites contained strains capable of growth on crude oil as a sole source of carbon (unconditional strains) along with strains that could degrade oil if proteose peptone was available in the growth medium (conditional strains). Additionally, the groups of isolates as a whole from each sample displayed remarkable similarities in the sizes of extrachromosomal elements, adhesion to crude oil, and hydrocarbon substrate utilization. The results indicate that common selection pressures may have produced groups of bacteria of different genera with similar physiologies at both sites.

Hydrocarbon degrading bacteria are widely distributed in nature (ZoBell 1946; Atlas 1981; Leahy & Colwell 1990). They may constitute up to 100% of the viable bacterial community in areas exposed to hydrocarbons (Atlas 1981). These communities develop at least partly from the autochthonous bacteria when the area is first exposed to hydrocarbons. The numbers and proportions of the hydrocarbonoclastic bacteria in the community will increase after exposure (Colwell & Walker 1977; Atlas 1981; Floodgate 1984; Cooney 1984). Eventually, only a few genera may dominate in the community (Llanos & Kjoller 1976); or, community diversity may remain unchanged (Pinholt et al. 1979; Olsen & Sizemore 1981) or even increase (Hood et al. 1975). These communities characteristically degrade hydrocarbons at higher rates than similar bacterial communities in unexposed areas (Leahy & Colwell 1990). In general they develop as the result of the availability of hydrocarbons for bacterial growth, apparently favoring strains that can grow on hydrocarbons over those that cannot. The predominance of hydrocarbon-utilizing bacteria may become permanent in areas subject to chronic exposure.

Petroleum-polluted environments also contain a much higher number of plasmid-bearing bacterial species than similar unpolluted areas (Hada & Sizemore 1981; Leahy & Colwell 1990; Ogunseitan et al. 1987). In Pseudomonas spp., the genes responsible for hydrocarbon degradation
often reside on plasmids. In these species the genes responsible for
degradation of toluates, camphor, salycilate, alkanes, and naphthalene
are found on, respectively, the TOL, CAM, SAL, OCT, and NAH
plasmids (Chakrabarty 1976). In other known hydrocarbon-degrading
bacteria such as Acinetobacter sp. HO1-N and A. calcoaceticus the
genes are located chromosomally (Singer & Finnerty 1984).

Interest in the degradative activities of hydrocarbonoclastic bacteria
in marine and terrestrial environments has produced many studies to
date. Not as much information has been obtained, however, on similar
bacteria found in freshwater systems. Furthermore, most studies have
been carried out in areas following accidental spills where selection
pressures exerted by the oil may be of relatively short duration.
Knowledge of the bacteria present in areas subjected to long-term,
chronic exposure is lacking and would be of scientific interest since
bacteria in these areas likely have formed stable associations. Oil
Springs, Texas is such an area of long-standing hydrocarbon exposure
(Pate 1987). This report characterizes hydrocarbon degrading bacteria
capable of heterotrophic growth in air from the oily mousse at two sites
there.

Materials and Methods

Site description and sampling.—The oil seepage was located in a
forested area about 25 miles southeast of the Stephen F. Austin State
University campus. Historical records indicate that as early as 1790
pioneers used the oil on the surface in this area for axle grease while
traveling westward (Pate 1987). The first producing well in Texas also
was drilled in this area in 1866.

Samples of oily mousse (biodegraded oil/water mixture) were
collected from two locations: 1) a site where crude oil seeps into a
small basin of freshwater and 2) the bank of a stream receiving crude
oil seepage. This stream also receives the discharge from the basin and
was sampled approximately 100 m upstream of that point. The two sites
are separated by a distance of approximately 200 m.

Isolation and identification of bacterial species.—Samples were
returned at ambient temperature (approximately 25°C) to the lab.
Approximately one gram was used to inoculate nutrient broth containing
10 gm/l crude oil as an enrichment for hydrocarbon-utilizing strains.
These 24 h cultures then were streaked onto nutrient agar (Difco) to
produce bacterial colonies. Preliminary sorting of isolates was carried
Table 1. Composition of growth media.

<table>
<thead>
<tr>
<th>Medium</th>
<th>Composition (gm/liter)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. SS(^a)</td>
<td>(NH(_4))(_2)SO(_4), (2); K(_2)HPO(_4), (14); KH(_2)PO(_4), (6); MgSO(_4), (0.2)</td>
</tr>
<tr>
<td>2. OSS</td>
<td>Crude Oil, (2); in SS</td>
</tr>
<tr>
<td>3. PPSS</td>
<td>Proteose peptone (Difco), (10); in SS</td>
</tr>
<tr>
<td>4. OPPSS</td>
<td>Crude Oil, (2); proteose peptone, (10); in SS</td>
</tr>
<tr>
<td>5. DSS</td>
<td>Diesel fuel, (2); in SS</td>
</tr>
<tr>
<td>6. MOSS</td>
<td>Mineral oil, (2); in SS</td>
</tr>
<tr>
<td>7. NSS</td>
<td>Naphthalene, (2); in SS</td>
</tr>
<tr>
<td>8. TSS</td>
<td>Toluene, (2); in SS</td>
</tr>
<tr>
<td>9. Luria agar</td>
<td>Tryptone, (10); yeast extract, (5); NaCl, (5); agar, (15)</td>
</tr>
</tbody>
</table>


out on the basis of colony and cellular morphologies, cellular arrangements, and Gram stain reaction. Each unique isolate then was identified by using a combination of the following tools: *Bergey’s Manual of Systematic Bacteriology*, John G. Holt (ed.), Williams and Wilkins, Baltimore / London; 20E and Rapid NFT Identification Systems (BioMerieaux-Vitek), and Microscan Rapid Identification System (Baxter).

**Media and growth conditions.**—The components of each growth medium are listed in Table I. All incubations were carried out at 25°C with vigorous shaking.

**Extrachromosomal DNA isolation and agarose electrophoresis.**—An isolation procedure designed to recover both large and small plasmids was used. Bacteria were grown overnight on Luria agar at 25°C. Approximately one square centimeter of cells was scraped from the plate and resuspended in 0.3 ml of lysis buffer containing 50 mM Tris-HCl and 3% (w:v) sodium dodecyl sulfate adjusted to pH 12.6 with 10 M NaOH. Cells were incubated at 60°C for 30 minutes. The resulting lysate was extracted with an equal volume of Tris-buffered phenol:chloroform (1:1, pH 7.5). The aqueous phase was recovered and electrophoresed through 1% (w:v) agarose gels in TBE buffer (89
Table 2. Degradation of crude oil and microbial adhesion to hydrocarbon (MATH) assays of bacterial isolates.

<table>
<thead>
<tr>
<th>Bacterial isolate</th>
<th>Amount of crude oil degraded(^a) (ppm) in each medium</th>
<th>MATH assay(^b) percentage decrease in optical density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OSS</td>
<td>OPPSS</td>
</tr>
<tr>
<td>Basin site</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. <em>P. aeruginosa</em>(^c) OSB1</td>
<td>1500-2000</td>
<td>1-500</td>
</tr>
<tr>
<td>2. <em>E. cloacae</em>(^c) OS2A</td>
<td>0</td>
<td>1500-2000</td>
</tr>
<tr>
<td>3. <em>A. faecalis</em> OS2B</td>
<td>1500-2000</td>
<td>1500-2000</td>
</tr>
<tr>
<td>4. <em>B. cereus</em> OS3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Stream site</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. <em>S. marcescens</em> CR2B</td>
<td>0</td>
<td>1000-1500</td>
</tr>
<tr>
<td>2. <em>E. americana</em> CRFW</td>
<td>1-500</td>
<td>1500-2000</td>
</tr>
<tr>
<td>3. <em>P. aeruginosa</em>(^c) CRFY1</td>
<td>1000-1500</td>
<td>1-500</td>
</tr>
<tr>
<td>4. <em>E. cloacae</em>(^c) CRFY2</td>
<td>0</td>
<td>1500-2000</td>
</tr>
<tr>
<td>5. <em>F. odoratum</em> CRLY</td>
<td>1000-1500</td>
<td>1000-1500</td>
</tr>
</tbody>
</table>

\(^a\) Starting concentration of crude oil was 2000 ppm. Values reported are in ranges consistently observed in several trials.

\(^b\) Measurements as described in Materials and Methods. Averages of three trials.

\(^c\) The two *P. aeruginosa* and the two *E. cloacae* isolates are different biotypes.

**mM Tris base, 89 mM boric acid, 2 mM EDTA.** DNA was stained with ethidium bromide and visualized with 254 nm wavelength UV light.

**Hydrocarbon utilization.**—Individual isolates were tested for the ability to utilize crude oil as a sole source of carbon and energy for growth by inoculating 100 ml of OSS broth (Table 1) with 0.1 ml of an 18-24 hour-old culture growing in PPSS broth (Table 1). OSS broth cultures were incubated seven days after which the remaining hydrocarbon was measured by infrared spectrophotometry according to *Standard Methods for the Examination of Water and Wastewater* (American Public Health Association 1990). In some experiments identical tests were conducted in PPSS broth. The ability to utilize diesel fuel, mineral oil, naphthalene, and toluene as sole sources of carbon and energy for growth was determined after incubation for seven days in DSS, MOSS, NSS and TSS broths (Table 1), respectively. Growth was considered positive if the cultures became turbid and dense populations of cells were detected microscopically.

**Microbial Adhesion to Hydrocarbon (MATH) Assays.**—MATH assays were carried out by a modification of the method of Rosenberg et al. (1980). Cultures that were 18-24 hours old were washed once and
resuspended in SS (Table 1). The density of the washed cultures was adjusted with SS to approximately 0.1 absorbance units at 600 nm wavelength. Two-tenths of a ml of crude oil was added to a 1.0 ml portion of the resulting suspensions which were then vigorously mixed for 120 seconds after which the hydrocarbon phase was allowed to separate from the aqueous phase for 15 minutes. The absorbance of the aqueous phase was measured. The percentage decrease in absorbance is a direct measurement of the percentage of cells removed from the suspension by adhesion to the crude oil.

Results

The four species of bacteria isolated from the basin and the five species from the stream site samples are listed in Table 2. All of these, with the exception of Erwinia, are common in freshwater habitats.

It is probable that other species were present in the samples and were not culturable by the enrichment and isolation procedure. The organisms that were isolated, therefore, probably do not constitute the entire bacterial community present in the oil.

A typical electrophoretic gel is shown in Figure 1. All of the strains tested, except Pseudomonas aeruginosa CRFY1, contained the smaller of the two size classes of extrachromosomal elements present. Additionally, Enterobacter cloacae OS2A and CRFY2, Serratia marcescens CR2B, and Erwinia americana CRFW all possessed the larger size class of element. No other size classes of elements were detected.

Each isolate was tested for its ability to utilize crude oil as a sole source of carbon and energy for growth in OSS broth (Table 2). Only P. aeruginosa OSB1 and Alcaligenes faecalis OS2B from the basin site and E. americana CRFW, P. aeruginosa CRFY1, and Flavobacterium odoratum CRLY from the stream site utilized the oil. The other species were unable to grow or degrade the oil in this medium. The inability of the species to grow in OSS apparently was due to inability to utilize the oil as a carbon source and not to a missing growth factor since all could grow in SS supplemented with 1% (w:v) glucose.

When similar experiments were conducted in OPPSS broth, which contains proteose peptone as an additional carbon source, degradation patterns changed for most of the isolates (Table 2). Degradation of the oil by the two P. aeruginosa isolates was reduced in this broth. This
Figure 1. Agarose gel indicating the extra-chromosomal DNA found in the bacterial isolates. Lanes 1 and 20 contain Hind III digested lambda phage DNA as a size standard. Sizes of the visible standard bands are indicated on the right of the figure. Lysate from each bacterial isolate was run in side by side lanes; even lanes contained 20 μl of lysate and odd lanes 40 μl. The species name for each isolate is given in Table 2. Both extrachromosomal DNA elements trail the 23 kb band of the lambda standard and are indicated by arrows. Several lanes also exhibit undegraded chromosomal DNA which co-migrates with the 23 kb standard band. Although not clearly visible, the presence of the larger element in CR2B was confirmed on other gels.

likely was due to repression of enzyme activity by constituents of the proteose peptone, a phenomenon which has been observed in this species during paraffin oxidation (van Eyk & Bartles 1968). Degradation by all of the other isolates increased markedly, except for F. odoratum CRLY and Bacillus cereus OS3 which remained unchanged. It is unknown whether the oil was utilized for growth or was degraded by cooxidation. All of the isolates grew vigorously in OPPSS and so failure to degrade the oil was not due to growth inhibition by components of the oil.

The experiments in OSS and OPPSS broths provide a basis for separating each isolate into one of three categories: unconditional degrader, conditional degrader, or non-degrader. The unconditional degraders can utilize oil as a sole source of carbon and energy. Isolates in this category are P. aeruginosa OSB1 and A. faecalis OS2B from the basin site and E. americana CRFW, P. aeruginosa CRFY1, and F. odoratum CRLY from the stream site. The conditional degraders can degrade oil when an additional carbon source is present, in this case proteose peptone. The isolates in this category are E. cloacae OS2A
Table 3. Growth of unconditional degrader strains on diesel fuel, mineral oil, naphthalene, and toluene as sole sources of carbon and energy.

<table>
<thead>
<tr>
<th>Isolate</th>
<th>Growth in each medium *</th>
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<tr>
<td></td>
<td>DSS</td>
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<tr>
<td>Basin site</td>
<td></td>
</tr>
<tr>
<td>1. <em>P. aeruginosa</em> OSB1</td>
<td>+</td>
</tr>
<tr>
<td>2. <em>A. faecalis</em> OS2B</td>
<td>+</td>
</tr>
<tr>
<td>Stream site</td>
<td></td>
</tr>
<tr>
<td>1. <em>E. americana</em> CRFW</td>
<td>+</td>
</tr>
<tr>
<td>2. <em>P. aeruginosa</em> CRFY1</td>
<td>+</td>
</tr>
<tr>
<td>3. <em>F. odoratum</em> CRLY</td>
<td>+</td>
</tr>
</tbody>
</table>

* growth, (+); no growth, (-). Growth was measured as described in Materials and Methods. See Table 1 for composition of media.

from the basin site and *S. marcescens* CR2B and *E. cloacae* CRFY2 from the stream site. The only non-degrader in either medium was *B. cereus* OS3 from the basin site.

Several attempts were made to induce growth of the conditional degraders and the non-degraders by culturing them in OSS broth in various combinations with the unconditional degraders (data not shown). All attempts failed; therefore, these species apparently cannot utilize the metabolites produced by the unconditional degraders during growth on oil. All species, however, could grow together in OPPSS broth and so growth inhibition of one species by another was not a factor in these results.

No correlation was found between utilization of crude oil by an isolate and the ability to adhere to crude oil (Table 2). Among the unconditional degraders, only *A. faecalis* OS2B and *F. odoratum* CRLY adhered. Neither of the *P. aeruginosa* isolates adhered, a finding which is consistent with previous reports on this organism (Rosenberg, 1991). However, during growth of these organisms the medium became foamy and the oil appeared to be emulsified. A bioemulsifier may therefore have been produced, allowing these strains to utilize the oil without adhering to it. The other unconditional degrader, *E. americana* CRFW, did not adhere. Of the conditional degrader strains, only *S. marcescens* CR2B was observed to adhere to crude oil; this finding is consistent as well with previous experiments with this species (Rosenberg 1991). The non-degrader strain (*B. cereus* OS3) also was non-adherent as has been observed previously (Rosenberg 1991).
The unconditional degrader strains were tested for the ability to utilize various components of crude oil. Mineral oil was chosen to represent a mixture of n-aliphatic compounds; diesel fuel was chosen to represent a mixture of straight and branched chain hydrocarbons; and naphthalene and toluene represented specific aromatics. Results are given in Table 3. There was remarkable homogeneity among the strains. All utilized diesel fuel; all but F. odoratum CRLY utilized mineral oil; and none was able to utilize naphthalene or toluene under the experimental conditions. The conditional degraders and the non-degraders were not tested.

Discussion

The oily mousse from the basin and stream sites contained different groups of bacteria. Although both samples contained a Pseudomonas aeruginosa and an Enterobacter cloacae strain, the strains from each were biotypically different from each other. No other cultured species were common to both samples. These assemblages of bacteria, therefore, appear to have formed independently.

The unconditional degrader strains represent species which are known to utilize crude oil for growth (Bartha & Atlas 1977) except for Erwinia, which to our knowledge has not been reported to do so. This isolate is unusual, therefore, and its presence in the oily mousse is unexpected since this genus is associated with plants in nature.

Notable similarities were found in the physiological categories of bacteria in the samples from both sites. Both contained unconditional and conditional degrader strains. Furthermore, among the unconditional degraders, there was almost complete homogeneity with respect to the substrates (diesel, mineral oil, naphthalene, or toluene) that can be utilized for growth. The unconditional degrader strains may be important hydrocarbon oxidizing strains at the sampled sites, while perhaps the conditional degrader strains also consume or cooxidize a portion while utilizing an additional carbon source for growth. The laboratory experiments do not indicate that the unconditional degrader strains can supply carbon for growth of the conditional strains in the form of hydrocarbon oxidation products.

The presence of extrachromosomal elements in the isolates from both sites is consistent with previous observations in other systems (Hada & Sizemore 1981; Leahy & Colwell 1990; Ogunseitan et al. 1987). In those systems, extrachromosomal DNA genes may have contributed to
the ability of the isolates to degrade oil. It is unknown at this point whether there is a similar function for the DNA in the Oil Springs isolates.

The presence of adherent strains in the samples is readily understood as cells of these organisms likely possess hydrophobic cell surfaces or fimbriae, or produce adhesins (Rosenberg 1991), which would maintain physical contact between the cell and the crude oil substratum. For example, the hydrophobic pigment, prodigiosin, of *Serratia marcescens* has been shown to increase adhesion of the cells to hydrocarbons (Rosenberg 1984) as well as has the serraphobin outer surface protein of this organism (Bar-Ness & Rosenberg 1989). *Serratia marcescens* CR2B produces the red pigment prodigiosin characteristic of the species and probably adheres at least for that reason.

The presence of hydrocarbon non-adherent strains may be explained by their adherence to organic particles within the oily mousse or co-adhesion to the adherent strains. *Pseudomonas aeruginosa* for example is well-known to produce exopolysachharides which allow it to form biofilms on a variety of surfaces. Cells of other species can become trapped in these biofilms as well (Wilderer & Characklis 1989).

The physiological similarities between the bacterial populations from the two samples may be a result of selection pressures exerted by the availability of the same crude oil at both sites. Crude oil from this location is high in C-20 or larger compounds with cyclic hydrocarbons present in lesser amounts (Pike 1977). The preference of the unconditional degrader strains for diesel and mineral oil likely reflects this content of the crude oil. Non-utilization of naphthalene and toluene by the isolates might be expected since cyclic hydrocarbons are not present in high amounts in this oil. This along with the hydraulic flow that moves bacteria and oil downstream away from the seep may inhibit strains capable of utilizing the cyclic portion from colonizing the oil at the seepage sites. Common selection pressures, therefore, appear to have produced the two different groups of hydrocarbonoclastic bacteria with similar physiologies at both sites, an expected outcome in stable, similar microenvironments. The unconditional strains do not appear to provide nutrients for the conditional strains and so the interaction between them in the oily mousse, if any, is not clear. Further investigations will reveal whether some other interaction exists and whether additional similarities can be found at the two seepages among the sediment and free aquatic bacteria not cultured in this study.
Acknowledgements

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Literature Cited


A NEW SUBSPECIES OF THE POLYTYPIC LIZARD SPECIES
SCELOPORUS UNDULATUS (SAURIA: IGUANIDAE)
FROM NORTHERN MEXICO

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Abstract.—Sceloporus undulatus belli is described from northern Mexico. This new
taxon represents the southernmost known subspecies and ranges from northwestern
Chihuahua to southern Coahuila, northwestern Zacatecas and northeastern Durango. In
northern central Chihuahua it occurs within a few km of the known range of Sceloporus
undulatus speari without evidence of intergradation. Sympatry is possible and at least close
parapatry appears likely. These two subspecies are assigned to different exerges; the new
taxon is assigned its own and is separate from the adjacent consobrinus exurge. The
relationships of the four exerges and 11 subspecies currently assigned to this species are
discussed, comparisons made, and a key proposed.

Taxonomic intraspecific parapatry is exemplified in the widespread
lizard species Sceloporus undulatus (Bosc & Daudin) in both primary (in
situ) and secondary (circular range approximation) contexts (Figure 1).
Instances of the former are numerous, but only two probable examples
of the latter have so far been noted.

In one example, S. undulatus garmani Boulenger and S. undulatus
erthrocheilus Maslin (of the consobrinus and tristichus exerges,
respectively) assuredly have closely approximated ranges in Baca and
perhaps Boulder counties, Colorado (Maslin 1964; Hammerson 1982).
So markedly different are these two taxa, even at their closest range
approximation (a few km) that they would qualify as distinct species
were it not for the indirect linkage provided by the obvious
intergradation of S. undulatus consobrinus Baird & Girard with not only
S. undulatus garmani but also with S. undulatus tristichus Cope, with
which S. undulatus erythrocheilus in turn clearly intergrades. Their
habitat preferences differ so strongly that at least macrosympatry could
occur.

The second example of circular range approximation occurs between
S. undulatus elongatus Stejneger and S. undulatus erythrocheilus in
southeastern Wyoming, where the former subspecies, otherwise limited
to western slopes, occurs in the upper reaches of the eastward-draining
Figure 1. Distribution of the subspecies of *Sceloporus undulatus*. Spots indicate localities represented by material examined in this study and in Smith et al. (1994), for *S. undulatus belii*, *S. undulatus consobrinus*, *S. undulatus speari* and *S. undulatus tristichus*. The X represents the isolated population here regarded as relictual intergrades between *S. undulatus garmani* and *S. undulatus consobrinus* (cf. Smith et al. 1993). The oval near the center of New Mexico represents an isolated population here referred to *S. undulatus tristichus*. The isolated population in southern Wyoming is referable to *S. undulatus elongatus* (cf. Smith & Nadvornik 1990). Base map courtesy Roger Conant. Range limits adapted from our own data, Conant & Collins (1991: map 70), Ferguson (1982:112, fig. 12), Smith et al. (1992:145, fig. 8), Hammerson (1982:70), Smith & Chiszar (1989:149, fig. 1), Smith et al. (1993:35, fig. 1), Stebbins (1985: map 86) and Applegarth (1969:51, fig. 3).
North Platte River, which passes through the range nearby, in much the same habitat, of *S. undulatus erythrocheilus*. At present the ranges of the two subspecies are known to come no closer than about 40 km, but the distribution of this species in this area is poorly known; the two subspecies probably occur considerably nearer to one another than is now apparent. Since they belong to the same exerge, and have the same habitat preferences, interbreeding rather than sympatry would be a likely outcome were their ranges to contact one another.

Both of these cases of circular range approximation involve populations whose ranges extend northward on either side of the natural barriers of the Rocky Mountains or the Great Plains.

No such examples, however, have been expected in this species in the southern part of its range, in the absence of comparable barriers and of known subspecific differentiation. It is therefore of great interest that this study of Mexican populations has revealed a third case of close range approximation without intergradation.

The recently described subspecies of the *consobrinus* exerge, *S. undulatus speari* Smith et al. (1994), is limited, so far as known, to the vast sand dunes of the northern central part of the state of Chihuahua. Only a short distance to the south and west of this area, and extending southeastward into Durango, Zacatecas and Coahuila, occurs a distinctly different subspecies bearing much the same geographic relationship to *S. undulatus speari* as *S. undulatus erythrocheilus* does to *S. undulatus garmani*. This new taxon is herein described. Specimens are deposited with the University of Colorado Museum at Boulder (UCM), the Museum of Comparative Zoology at Harvard (MCZ), the University of Michigan Museum of Zoology at Ann Arbor (UMMZ), the University of New Mexico Museum of Southwestern Biology at Albuquerque (MSB) and the University of Texas at El Paso (UTEP).

*Sceloporus undulatus belli*, new subspecies
(Figures 2 & 3)

**Holotype**—Adult male (UCM 41539), 2 mi S of León Guzmán, Durango, México, 19 June 1966, collected by Richard L. Holland.

**Paratypes**.—One hundred and fifty-six specimens in the following museums.

**MCZ.**—Six specimens, all from Chihuahua: 32.5 km ESE Cd. Cuauhtemoc, 1850 m (126874); 12.5 km SE Moctezuma (126854); 16
km SSE Moctezuma (126855-7); 2 km W Ricardo Flores Magón, 1485 m (126933).

**UMMZ.**—Three specimens, all from *Chihuahua*: 11 mi W Cd. Cuauhtemoc, 6850 ft (118971A-B); 30 mi S El Sueco, 4700 ft (118972).

**MSB.**—20 specimens, all from *Chihuahua*: 16 mi E Aldama, Hy 16 (33222, 33411); 4.5 mi S Cd. Camargo, Hy 45 (7196-7); Cd. Chihuahua, International Airport runway (39945); jct Hy 16 and 45, SW Cd. Chihuahua (56335); 20.5 mi N Cd. Chihuahua, Hy 45 (8956-7); 17.1 mi W El Carmen (8968); 9.1-9.3 mi S El Sueco, Hy 45 (8961, 8966); General Trías, centro (33223); Ojo de los Reyes, 4.7 mi SE Galeana, 1 mi N Angostura (39946-7); ruins of Paquimé, Casas Grandes Viejo (35041-2); 9 mi SE Río Florida in Jiménez (8922); 15 km E, 7 km N San Buenaventura, Hy 10 (35043-5).

**UCM.**—70 specimens, from Chihuahua and Durango: *Chihuahua*: 15.6 mi S Cd. Chihuahua (41504); 22 mi S Cd. Chihuahua (41505-13); 3 mi S Encinillas (24285); 7 mi NE Escalón (16812-4, 16816-8); 18 mi...
Figure 3. Ventral views of the same specimens as in Figure 2. Note the typical, unmarked venter of this large female, and the typical, extensively fused gular semeions, with no anterior or medial edging with black, in the large male.

S Gallegos (16801-11); S Jiménez (41518); 7 mi N Jiménez (49677); 7 mi S Jiménez (49516-7); 12.5 mi S Jiménez (41519-32); Meoqui, S side Río San Pedro (41514); 8.6 mi S Moctezuma (41502-3); 2.5 mi S Saucillo (41515). Durango: 2 mi N Cuencamé (41535-7); 20.4 mi S Cuencamé (41538); 19 mi SW Gómez Palacio, Río Nazas, 3800 ft (51414); León Guzmán (41542); 1.1 mi N León Guzmán (41534); 1.7 mi SW León Guzmán (41540-1); 5 mi NE Pedriceña (50001); 17 mi S Rodeo, 5500 ft (24286).

**UTEP.**—57 specimens, from Chihuahua, Coahuila, Durango and Zacatecas. Chihuahua: Aldama, 20.3 rd mi NE, Hy 16 (9238); Ascención, 9.9 rd mi SW (4271); Camargo, 1 mi E (4513); Camargo, 15 mi N (4536); Camargo, 15 mi S, Hy 45 (9443); Camargo, 16 mi W, Presa Boquilla (9442); Cd. Chihuahua, 4 km NW, Lago Jacales (9441); Cd. Chihuahua, 5 km NW, Casa Salud (9437-40); El Sauz, 11 mi SSE turn-off to, Hy 45 (4518-20); El Sauz, 16 mi NNE turn-off to, Hy 45 (4537-8); El Sueco, Hy 10 3.2 km WNW jet Hy 45 and 10 (14514);
Escalon, 13 rd mi NW, Hy 49 (9236); Gallego, 1.5 mi N (4529-30); Gallego, 6 mi S (4531); Jiménez, 20 mi SE (4515-7); La Perla, 15.2 rd mi N (9237); Parral, 7 mi E (4512); Ricardo Flores Magón, Río del Carmen (4514). Coahuila: El Chiflón, 36 km W Saltillo, Hy 40 (4459, 6707-8, 6783-5); Francisco E. Madero (Chávez), 3 km E, Hy 30 (6779, 6811, 7567-8). Durango: Atotonilco (4532-3); Ceballos, 2 mi SE (4539); Ceballos, 2.4 mi E (6415); Mapimí, 17.7 mi W, Hy 30 (4525-6); Sombreretillos, 7.9 rd mi SE (9514); Zavala, 6.4 mi SE, Hy 49 (4524). Zacatecas: Anáhuac, 2 km E (4460); Anáhuac, 3 km E (6802-6); Anáhuac, 6 km E (7465); Camacho, 27.8 mi NE, rd to Mazapil (9445); Cinco de Mayo, 5 km NE (4446); La Presa de Junco, 3.5 rd mi W, 24°17′45″ N, 101°41′45″ W (3612); Río Grande, 13 rd mi SSE (4540-1).

Range (Figure 1).—Extreme northwestern Chihuahua (only ~50 km from Hidalgo County in the southwestern corner of New Mexico) southeastward east of the Sierra Madre Occidental through central Chihuahua to northeastern Durango, and eastward through northwestern Zacatecas and southern Coahuila.

Diagnosis.—A member of the polytypic species Sceloporus undulatus, assigned to its own monotypic exerge (refer to Recommendation 6B of Article 6 of of the International Code of Zoological Nomenclature 1985, for use of this term in lieu of "subspecies group"), distinguished by the combination of usually poorly developed dorsolateral light lines; conspicuous dorsal crossbars in females, but usually a nearly unicolor, unmarked dorsum in males, with a broad, conspicuous lateral dark line (a sexual dimorphism unique to the subspecies); almost invariably, complete absence of ventral markings in females except for small, dim and diffuse gular semeions in about half of the specimens; blue component of gular semeions always fused, usually fully but at least in part in all males except juveniles (<45 mm SVL; unique to the subspecies), not or weakly black-bordered anteriorly or medially. Differences from other subspecies are summarized in the following sections on Relationships, Subspecific Key and Adjacent Subspecific Comparisons.

Description of Holotype.—An adult male (Figures 2 & 3), 68 mm SVL. Four postrostrals; four internasals in a row between middle of nasals; three scales on either side of midline between median frontonasal and rostral; frontonasals in contact side to side, not subdivided; prefrontals in median contact, not subdivided; frontal in two parts,
anterior and posterior, not further subdivided; interparietal and frontal in contact; 1-1 frontoparietals. Supraoculars 5-5; 8-9 oculociariies; 1-1 subnasals, separated by one row of lorilabials from supralabials; 2-2 canthals, in normal position; 1-1 preoculars; lorilabial rows reduced to 1-1 by at least one scale below subocular; loreals 1-1.

Outer labiomental row ending anteriorly opposite 1-1 infralabials, inner row opposite 3-3 infralabials.

Dorsals 39, minimum count interparietal to level of rear margin of thighs held at right angles to body axis; femoral pores 17-18; interfemoral pore scales six.

Dorsal ground color a light tan, without a dorsolateral series of dark spots; a well-defined lateral line, dark brown, 1-3 scale rows wide, not sharp-edged, from orbit to base of tail, narrowest on neck, widest at midabdomen, bordered medially by a dim dorsolateral light line one and two half scale rows wide; a broad, grayer vertebral area four and two half scale rows wide. Sides of abdomen below lateral dark line light tan, merging ventrally with the light blue abdominal semeions (AS) that extend between levels near axilla to near groin; a narrow medial black border on AS, not reaching either axilla or groin; a minimum of four scales between AS black borders. No black flecks on chest, inter-AS abdomen, or ventral surfaces of limbs or tail.

Gular semeions (GS) mostly light blue, narrowly bordered posteriorly by an extension from a black patch in each nuchal pocket, extending toward but not onto foreleg. No black pigment bordering GS anteriorly or on sides, and none anterior to GS. A short, narrow, black divider posteriorly between the right and left halves of the GS, and a dim, median whitish indentation anteriorly between the two blue halves.

Variation.—The most conspicuous deviation from the preceding description occurs in female coloration. Females invariably have a dorsolateral series of dark spots (Figure 2); in a few specimens (e.g., UCM 16809, 41522) they are fused to form a more or less continuous dorsolateral dark line. Typically some or all of the spots form transverse bars that cross the dorsolateral light line, and where this occurs, frequently a bright light spot in the dorsolateral light line lies immediately posterior to the crossbar. A narrow lateral light line is often present, bounded ventrally in some specimens with a still narrower, irregular sublateral dark line, and dorsally by the area occupied in males by the lateral dark line, which is typically poorly defined in females.
On the contrary, males are usually essentially unicolor light brown between the lateral dark stripes, with no dark markings whatever or, at most, a few very narrow, dark, longitudinal streaks. The dorsolateral light lines are typically obscure in fully mature males, distinct in juveniles. The lateral dark line is invariably broad, continuous and uninterrupted. A lateral light line is usually present ventral to the lateral dark line, and is bordered ventrally by a narrow, sublateral dark line. Some males, typically young (e.g. UNM 8961, 8966, 35043, 35045, 39947, 56335) are exceptional in having a dorsolateral series of dark marks; in most they are much less prominent than in females, but they do interrupt the dorsolateral light line.

Sexual dichromatism is equally conspicuous ventrally (Figure 3). With one exception (UTEP 4524), no female has a well-defined GS, and less than a third (18 of 63) exhibit any evidence whatever of them; in the mentioned exception they are distinct but small and fused. In one other they are clearly evident, but weak, and in the others they are very dim, diffuse and widely separated. In only one of 63 (the same exception, UTEP 4524, noted previously) is there any evidence whatever of AS; in that exception they are poorly defined but certainly visible. Otherwise the only dark markings are a very narrow midventral streak, often interrupted or faint, or both, and in a few specimens a few similar streaks on throat or chest.

All males, on the contrary, with a SVL of 43 or more (81), have conspicuous AS and GS, with the exception of one (of two) at 43 mm SVL; that exception, and four smaller ones, show no evidence of either GS or AS. The blue components of the GS are fused in every male, although their basically paired nature is frequently evidenced by a partial median division. In no other subspecies are the blue components of the GS fused; if the GS are fused at all, it is the black borders that are involved. The AS are invariably separated, by a minimum of 1-7 scales (one, 2; two, 4; three, 8; four, 18; five, 14; six, 7; seven, 1). Usually no dark ventral pigmentation, other than the AS, occurs on chest, midabdomen or legs, except for the fine midventral line and dim streaks on chest of a few. The AS extend onto the thigh in the largest specimens, and the GS barely reach the foreleg in a few. The GS are bordered posteriorly (but seldom anteriorly or medially, and narrowly in those exceptions) by black or dark blue (not readily distinguishable) in some, and some brown pigment is scattered over the throat anterior to the GS in most specimens.

Thus, unlike other subspecies of *S. undulatus, S. undulatus belli* has
the two sexes trenchantly distinguishable in almost all fully mature adults in both dorsal and ventral color/pattern; this is a unique feature of the subspecies.

Variation in scalation does not appear to be sexually dimorphic, hence the following data are not sorted by sex. Postrostrals usually (84) four, three in six, two in two. Internasals in a row between nasals usually (85) four, three in one, two in four. Scales between median frontonasal and rostral, on either side of median line, usually (64) 3-3, 2-2 in three, 2-3 in six, 3-4 in eight, 4-4 in six. Frontonasals usually (82) undivided and in serial contact, subdivided or separated on one or both sides in eight. Prefrontals usually (50) in contact medially, separated by an azygous scale in 24, by contact of frontal and median frontonasal in 17. Frontal usually (78) divided into anterior and posterior sections, without subdivision, abnormal (subdivided, undivided or with anomalous fusions) in 12. Frontal usually (79) in contact with interparietal, separated by an azygous scale in two, by contact of frontoparietals in nine. Frontoparietals usually (76) 1-1, but 1-2 in 11, 2-2 in two, 2-3 in one. Supraoculars most frequently (25) 5-5, but 5-6 in 20, 5-7 in two, 6-6 in 23, 6-? in two, 6-7 in five, 7-7 in 12, 8-8 in one. Total (both sides) oculociliaries 14 (three), 15 (one), 16 (three), 17 (five) 18 (eight), 19 (five), 20 (five), 21 (seven), 22 (ten), 23 (seven), 24 (nine), 25 (three), 26 (six), 27 (five), 29 (three), 30 (six), 31 (one), 32 (one). In 6 of 83 specimens, one or more supraoculars are in at least narrow contact with one or more median head scales on one or both sides. The subnasal is abnormal in three of 88 (1-2 in one, fused with anterior canthal on one side of two). The canthals are normal in 71; the first is displaced dorsally on one side in three, is in contact with the lorilabials on one side in five, both sides of eleven, fused with the loreal on both sides in two, one side in two, and fused with subnasal on one side of two. The preoculars are 1-1 in 81, 1-2 in four, 2-2 in two, 2-3 in three. The two rows of lorilabials between subocular and supralabials are complete, or are reduced to one at some point on one or both sides as follows: 1-1, 32; 1-2, 20; 2-2, 36; 1-, 1; 2-, 2. The loreals are 1-1 in 74, 1-2 in 6, 2-2 in 4, 2-3 in one, 3-3 in one, and are fused with the first canthal on both sides in two, one side in two. The outer labiomental row extends anteriorly to the mental (M) or to the level of the 1st or 2nd infralabial as follows: 1-1, 77; 1-, 2; 2-2, 1; M-1, 5; M-M, 5; M-, 1. The inner labiomental row extends anteriorly to the levels of the 2nd, 3rd or 4th infralabials as follows: 2-2, 1; 2-3, 2; 3-3, 84; 3-4, 2.

Dorsal scale count 35-44 (35, one; 36, one; 37, four; 38, eight; 39,
thirteen; 40, twelve; 41, eighteen; 42, fifteen; 43, ten; 44, four). Femoral pores 14-20 (14, ten; 15, twenty-eight; 16, sixty-two; 17, fifty; 18, twenty-one; 19, eight; 20, two). Minimal scale count between femoral pore series, 3-8 (three, 1; four, 18; five, 34; six, 26; seven, 8; eight, 2). Lamellae under free part of 4th toe 20-24 (20, two; 21, eight; 22, four; 23, three; 24, three).

SVL parameters (in mm) in the 54 males (and parenthetically in the 37 females) are: range, 43-74 (52-77); 40-49, 1(0); 50-59, 17 (9); 60-69, 32 (21); 70-77, 4 (7).

Etymology.—The subspecies is named for Dr. Edwin L. Bell, a retired Professor of Biology at Albright College, Reading, Pennsylvania, in recognition of his meticulous study of geographic variation in the western member, *S. occidentalis*, of the *undulatus* exerge. He also first observed and brought attention to the distinctness of the present taxon.

Habits and Habitat.—The authors have had no experience with this subspecies in the field. Tanner (1987: 396) stated that most specimens he there reported of "*S. undulatus consobrinus*" (all 46 now referable to *S. undulatus belli* except for one *S. undulatus speari* from 30 mi S Cd. Juárez) were "seen and collected ... along the valley roads, many of them sunning on rocks and mounds of soil which had been left as the roads were constructed." Dr. Robert G. Webb, who has observed the species over many years in Chihuahua, states (pers. comm.) that "The *S. undulatus* in eastern Chihuahua south of El Sueco into northeast Durango are generally ground-dwellers in areas of small bushes, shrubs and ground debris. The general area is grassland with scattered shrubs that may be mesquite, creosote, acacia and/or cholla, the terrain either flat with hard-packed clay soils or more hilly with a rocky substrate. During inclement weather (overcast, windy, rather cold with rain threatening) lizards have been found under rocks. In looking at my field notes, occasional specimens have been noticed on fence posts, associated with cement-supported road culverts, and a few inches above ground on low shrub branches."

Field notes on UMMZ 118971(2) from 11 mi W Cuauhtemoc, Chihuahua, state that the specimens were taken at 6850 ft., in steep, rocky hills of a pass, where there were oaks and some pines and junipers, with bushes and weeds between rocks. UMMZ 118972 from 30 mi S El Sueco, Chihuahua, was taken at 4700 ft., on bushy flats with scattered clumps of weeds and grass amongst tall mesquite trees, with bare earth between; the lizard was asleep in a bush.
Intensive searches for *S. undulatus* conducted as a part of this study from Sept. 28 - Oct. 4, 1993 (Lemos-Espinal et al. 1994) in the extensive sand dunes east and west of Hy 45 south of Cd. Juárez, as far south as El Sancho, revealed only *S. undulatus speari*, no *S. undulatus bellii*. It appears certain that the latter does not occur in the dunes area, although it is here recorded from as near as 12.5 km SE Moctezuma, and farther west it occurs as far north as does *S. undulatus speari*. Whether either subspecies occurs in the intervening territory remains to be determined.

**Relationships**

This study retains the same taxa and exerges as proposed by Smith et al. (1992), but adds another exerge to accommodate *S. undulatus bellii*, adds *S. undulatus speari* to the *consobrinus* exerge (as proposed by Smith et al. 1994), and indicates the proposed derivation of each taxon as indicated primarily by the existence of intergradation. None is known between *S. undulatus speari* and its presumed ancestor, *S. undulatus consobrinus*, but may well occur in areas between the known limits of their geographic ranges, whence no material is now available although no barrier to the occurrence of the species appears to exist.

*Sceloporus undulatus bellii*, with its relatively large size, cross-barred females, usually unspotted males, almost complete lack of ventral markings in females, the light gular semeions with their unique fusion of the blue components in mature males, and its terrestrially cursorial habits and habitat, fits with none of the other exerges.

The *undulatus* exerge is limited to eastern North America, hence is not involved, although it is different in being scansorially arboreal, cross-barred dorsally and more heavily pigmented ventrally in both sexes. Members of the *consobrinus* exerge are relatively small, their dorsolateral light stripes tend to be bright, dorsal spotting is usually present in both sexes except in the bleached, arenicolous taxa, and all are terrestrially cursorial. Members of the *tristichus* exerge tend to have distinct, dark dorsal crossbars or spots in both sexes, are scansorially rupicolous, are heavily pigmented ventrally in both sexes, and are relatively large.

**Subspecific Key**

*Sceloporus undulatus consobrinus* appears twice in this key, in adjustment to the variation in the intensity of the dorsolateral light stripe, consistently bright in eastern populations, but subdued in some western
intergrade populations, through the influence of *S. undulatus tristichus*. *Sceloporus undulatus speari* likewise appears twice to account for the difference between the bleached summer dorsal pattern and the darker winter one.

1A. East of the Mississippi River and dorsal scale count, interparietal to level of rear margins of thighs held at right angles to base of tail, less than 38 (92%; Smith, 1938) .................................. *S. undulatus undulatus*
B. Not as above ......................................................... 2

2A. Dorsal count 46 or more (86%; Smith 1938) .................. *S. undulatus elongatus*
B. Fewer (>85%; Smith, 1938, and present data) .................. 3

3A. Dorsum bleached, whitish ........................................ 4
B. Not as above ......................................................... 6

4A. Gular semeions absent or vestigial in both sexes; maximum SVL 54 mm in males, 59 mm in females .......................... *S. undulatus tedbrowni*
B. Gular semeions well developed, at least in males; maximum SVL 60-64 mm in males, 69 mm in females .......................... 5

5A. Semeions not black-bordered ..................................... *S. undulatus speari*
B. Semeions black-bordered .......................................... *S. undulatus cowlesi*

6A. Gular semeions absent in both sexes ................................ *S. undulatus garmani*
B. Gular semeions prominent at least in males .................... 7

7A. Females without ventral markings, or with only dim, diffuse gular semeions, and boldly cross-barred dorsally; fully adult males usually without dark marks dorsally, blue components of gular semeions at least partially fused, usually not black-bordered medially or anteriorly .................. *S. undulatus belli*
B. Not as above ......................................................... 8

8A. Dorsolateral light lines distinct, broken or not ................ 9
B. Dorsolateral light lines poorly defined, broken ................. 10

9A. Semeions not black-bordered in either sex .................... *S. undulatus speari*
B. Semeions black-bordered .......................................... *S. undulatus consobrinus*

10A Black-bordered abdominal semeions present in both sexes .................................................. *S. undulatus tristichus*
B. Abdominal semeions not present in females, or if present not black-bordered .................................................. 11

11A Dorsum prominently cross-barred; venter with scattered black pigment .................................................. 12
B. Not as above ......................................................... *S. undulatus consobrinus*

12A West of the Great Plains; males with lips and throat reddish or yellowish at least in breeding season .................. *S. undulatus erythrocheilus*
B. East of the Great Plains; no red or yellow on head in either sex at any season .................................................. *S. undulatus hyacinthinus*

Adjacent Subspecific Comparisons

As indicated in the preceding key to subspecies, the standard criteria of dorsal pattern, ventral pattern, size and habits/habitat provide most
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The number of *S. undulatus belli* is followed parenthetically by the number of *S. undulatus tristichus*. Sequence the same in percent column. Diagnostically significant differences are indicated by an asterisk. See text for character-states.

character-states readily differentiating the eleven recognized subspecies from each other. Dorsal scale count is useful in distinguishing *S. undulatus undulatus* and *S. undulatus elongatus* from all other subspecies, and from one another, but scalation has been little utilized otherwise in subspecies characterization. Data taken on certain features of external morphology of the four subspecies of immediate concern relative to *S. undulatus belli* (*S. u. consobrinus, S. undulatus speari, S. undulatus tristichus*) reveals that a few diagnostically useful as well as significant but individually non-diagnostic differences between those taxa do exist among those features, as well as in the standard criteria. Hence these subspecies are demonstrably more than mere pattern classes.

Chi-square values of all compared morphological characteristics are given in Tables 1-5, where the character-states are given the following numbers: tail/total length ratio (1) .58 or more, or (2) .59 or more, or (3) .60 or more, or (4) .62 or more; dorsal scale count (5) 39 or less, or (6) 41 or less, or (7) 41 or more; scales between femoral pore series (8) five or more; internasals in a line between median frontonasal and rostral, on each side of median line, (9) 3-3 or more; prefrontals (10) separated medially; frontal (11) separated from interparietal, or (12) abnormal (fused, subdivided, etc.); frontoparietals (13) more than 1-1; supraoculars (14) 5-6 or more, or (15) 5-7 or 6-6 or more, or (16) one or more in contact with median head scales on one or both sides; total oculociliaries, on both sides, (17) 19 or more, or (18) 20 or more; canthals (19) with the 1st contacting lorilabials on one or both sides, or (20) abnormal (fused, subdivided, contacting lorilabials, or displaced); preoculars (21) 1-2 or more; lorilabials below subocular (22) in two
Differing character-states in a single character in the preceding list, e.g. 1-4, 5-7, etc., were selected ad hoc for maximum discrimination between the particular compared taxa, and would be useless in comparison of certain other taxa. Table 6 documents the variation of all 23 selected character-states in the four subspecies of present concern. Because many statistical tests were conducted, it was inappropriate to evaluate all of them at the 0.05 level of significance, as this could have elevated the rate of type I errors to an unacceptable level. To protect the over-all error rate, individual comparisons were judged to be significant at the 0.005 level (Kirk 1982:101-106).

Sceloporus undulatus belli, for example, is diagnostically distinguished from S. undulatus tristichus (from whose range it is narrowly separated by the western arm of S. undulatus consobrinus; see Figure 1), the nearest subspecies of comparable size (maximum SVL 71 mm in males, 75 mm in females, vs 74 mm and 77 mm, respectively,
Figure 5. Ventral views of *S. undulatus tristichus*. Upper, male, same as in Figure 4. Lower, female (UCM 7635, 64.5 mm SVL, 5 mi E Gallina, Rio Arriba Co., New Mexico). Note the medial and anterior black borders of the gular semeions in the male, and the remarkably masculine markings of the female.

in *S. undulatus belli*) and with reduction of the dorsolateral light stripes, in three morphological characters, and, in addition, statistically significant differences exist that are not individually diagnostically useful in four others (see Table 1). Five pattern differences are easier to evaluate (although less objective) and are the primary basis for distinguishing these two subspecies (Figures 2-5): (1) complete separation of gular semeions in males (0% in *S. undulatus belli*, 71% in *S. undulatus tristichus*); (2) gular semeions absent or faint in females (100% in *S. undulatus belli*, 5% of *S. undulatus tristichus*); (3) absence of any indication of abdominal semeions in females (100% in *S. undulatus belli*, 0% in *S. undulatus tristichus*); (4) absence of black median and anterior borders of the gular semeions in males (100% of *S. undulatus belli*, 0% of *S. undulatus tristichus*); and (5) absence of scattered black pigment on venter (95% in *S. undulatus belli*, 0% in *S. undulatus tristichus*). In addition, *S. undulatus belli* is reputedly terrestrial and cursorial, *S. undulatus tristichus* petricolous and scansorial.
Figure 6. Dorsal views of *S. undulatus consobrinus* from the western arm of the subspecies' distribution, in southeastern Arizona. Left, female, UCM 56071, 55 mm SVL, Santa Cruz Co., 5 mi SE Elgin. Center, a female, UCM 56884, 62 mm SVL, Santa Cruz Co., Audubon Research Ranch, 6 mi SSE Elgin. Right, a male, UCM 56886, 64 mm SVL, same locality as the preceding.

No scalation features distinguish *S. undulatus belli* from *S. undulatus consobrinus*, although the latter is smaller (74 mm SVL maximum and 67% 60 mm or more in males, and 77 mm, 76% 60 mm or more in females of *S. undulatus belli*; 72 mm and 27% 60 mm or more in 131 males, and 74 mm, 39% 60 mm or more in 122 females of *S. undulatus consobrinus*). The primary distinctions are in pattern (Figures 2-3, 6-7), *S. undulatus belli* having (1), with rare (one) exception, gular semeions faint or absent in females (vs distinct); (2) usually no anterior or medial black borders on broadly fused, blue gular semeions in males (vs present, blue not fused); (3) dorsolateral light stripes usually absent or poorly defined in fully mature adults (vs well defined throughout life); and (4) a strong sexual dimorphism in dorsal pattern, females being brightly cross-barred, males unspotted and unicolor between lateral dark lines (vs no distinct pattern dimorphism, both sexes spotted or cross-
barred dorsally). Four significant but individually non-diagnostic differences exist; see Table 2.

Similarly, no scalation features distinguish S. undulatus belli from S. undulatus speari, although the latter is smaller (74 mm SVL maximum and 67% 60 mm or more in males, 77 mm, 76% 60 mm or more in females of S. undulatus belli; 64 mm and 14% 60 mm or more in males, 69 mm and 38% 60 mm or more in females of S. undulatus speari). Three statistically significant but independently non-diagnostic morphological differences between the two subspecies occur, however; see Table 3. Pattern differences are diagnostic (see figures in Smith et al. 1994), with S. undulatus belli (1) having the dorsolateral light lines usually absent or poorly defined, at least in fully mature adults (vs well developed); (2) a strong sexual dimorphism in dorsal pattern, with females strongly barred and fully adult males usually without dark marks
Table 2. Chi-square values and percent occurrences for statistically significant morphological differences between *S. undulatus belli* and *S. undulatus consobrinus*

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The number of *S. undulatus belli* is followed parenthetically by the number of *S. undulatus consobrinus*. Sequence the same in percent column, where none are of individual diagnostic significance. See text for character-states.

...and with a unicolor dorsum between the lateral dark lines (vs the same striped pattern in both sexes); (3) 100% of the males with the gular semeions in contact (vs 21%); and, significantly but non-diagnostically, 1% of females with distinct gular semeions (vs 35%).

The most distinctive single feature of *S. undulatus belli*, distinguishing it not only from the three subspecies most closely associated geographically, dealt with in the three preceding paragraphs, but from all others of the species, is the fusion, partial or complete (usually the latter), of the blue components of the GS in adult and subadult males. In all other subspecies the GS are either completely separated or have their black borders fused.

Comparisons of *S. undulatus consobrinus* with *S. undulatus speari* are given in the description of the latter (Smith et al. 1995). The latter was not compared in detail with *S. undulatus tristichus*, however. Three diagnostically significant morphological differences and five individually non-diagnostic morphological differences exist (see Table 4). Size differs somewhat; in *S. undulatus speari* the maximum SVL in males is 64 mm, and 14% are 60 mm or more in SVL (in females, 69 mm and 38%), whereas in *S. undulatus tristichus* those figures are 71 mm and 22% for males, 69 mm and 55% for females. Three diagnostically significant differences exist in pattern; *S. undulatus speari* has (1) distinct dorsolateral light lines (vs faint); (2) no black borders on its semeions (vs present); and (3) abdominal semeions faint or absent in 100% of females (vs distinct, in no less than 89%, but probably close to 100% excluding possible intergrades). Non-diagnostically but statistically significantly, no more than 35% of *S. undulatus speari* females have distinct gular semeions, whereas at least 95% of *S. undulatus tristichus* females do.
Table 3. Chi-square values and percent occurrences for statistically significant morphological differences between *S. undulatus belli* and *S. undulatus speari*

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The number of *S. undulatus belli* is followed parenthetically by the number of *S. undulatus speari*. Sequence the same in percent column, none of individual diagnostic significance. See text for character-states.

Finally, although Applegarth (1969) synonymized *S. undulatus tristichus* with *S. undulatus consobrinus*, this study provides ample evidence that they are distinct taxa (allosubspecific). The only structural difference at a diagnostic level that was found is in tail/total length ratio, but statistically significant differences of independently non-diagnostic magnitude exist in at least six features of scalation (see Table 5). The other diagnostically significant differences lie in pattern: in *S. undulatus consobrinus*, (1) 29% of males have the gular semeions separated (vs 71% in *S. undulatus tristichus*); (2) in 100% of females, abdominal semeions are absent or faint (vs at most 11%, most of which are probably intergrades); and (3) all except intergrades have distinct dorsolateral light lines (vs indistinct lines).

A distinct difference between these two taxa also exists in habits and habitat, *S. undulatus consobrinus* being cursorial and terrestrial, *S. undulatus tristichus* scansorial and saxicolous (personal observation).

Future Research

The intricate populational relationships of the subspecies currently recognized in *S. undulatus* are likely to require study for many years to come. In particular, the wide-ranging subspecies *S. undulatus consobrinus* and *S. undulatus hyacinthinus* merit further study of geographic variation. The taxonomic rank of the four exerges, particularly of *belli* and *undulatus*, need attention. The taxonomic status of the relic population near Limon, Colorado (Smith et al. 1993), remains enigmatic (although here viewed as relic intergrades between *S. undulatus garmani* and *S. undulatus consobrinus*), and the possible sympatry of several terminal populations is intriguing. Areas of intergradation are in need of refinement in almost every case. The plethora of subspecies in New Mexico (certainly six, and possibly seven
Table 4. Chi-square values and percent occurrences for statistically significant morphological differences between *S. undulatus speari* and *S. undulatus tristichus*

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The number of *S. undulatus speari* is followed parenthetically by the number of *S. undulatus tristichus*. Sequence the same in percent column. Diagnostically significant differences are indicated by an asterisk. See text for character-states.

or eight if *S. undulatus speari* and/or *S. undulatus belli* occur there) is an open invitation for study. Applegarth’s review (1969) of northeastern populations in the state did not distinguish *S. undulatus consobrinus* and *S. undulatus tristichus*, but did not consider sexual dimorphism in ventral coloration.

A further problem exists in the sexual dimorphism in dorsal pattern in *S. undulatus belli*; this is a character unprecedented in the *S. undulatus* complex. Its phylogenetic origin and adaptive value are completely unknown. Also, *S. undulatus speari* presents a unique, presumably hormonal adaptation that permits a bleached dorsal pattern in summer to be replaced in the fall with a darker pattern that enables even adults, which in other species have gone into hibernation (or brumation), to remain as active as in midsummer (Smith et al. 1995). No intergradation of *S. undulatus speari* with other subspecies has been confirmed and needs investigation. Morrison’s (1988) study concludes with allospecificity of *S. undulatus hyacinthinus* on one hand, and *S. undulatus garmani* plus *S. undulatus consobrinus* on the other. On the contrary, McCoy (1961) found all three subspecies intergrading in limited zones in Oklahoma. Further study is needed for a definitive conclusion.

Although the *undulatus* and *tristichus* exerges appear to be parallel lines of evolution, separated by the *consobrinus* exerge (Figure 1), there appears to be no reason to question the conspecificity *S. undulatus tristichus* and *S. undulatus consobrinus*, because of the occurrence of intergradation between them in central and southern New Mexico and
Table 5. Chi-square values and percent occurrences for statistically significant morphological differences between *S. undulatus consobrinus* and *S. undulatus tristichus*

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</tbody>
</table>

The number of *S. undulatus consobrinus* is followed parenthetically by the number of *S. undulatus tristichus*. Sequence the same in percent column. Diagnostically significant difference indicated by an asterisk. See text for character-states.

southern Arizona. Intergradation is indicated by the shift in females from absence of abdominal semeions (*S. undulatus consobrinus*) to presence of them (*S. undulatus tristichus*), by the shift in both sexes from bright dorsolateral light lines (the former) to their reduction or loss (the latter), and by the shift from terrestrial to petricolous habitats, respectively. Attention is called to the intergrades from Bernalillo (15 mi E Albuquerque; 2-4 mi N Isleta Pueblo), San Miguel (2.3 mi W Sands) and Santa Fe (3 mi N Peña Blanca; 5-9 mi E Santa Fe; 9 mi S Santa Fe) counties, all referred to *S. undulatus consobrinus* although with very weak AS in females. No records indicate whether any of these specimens were in a terrestrial or petricolous habitat. A series of seven specimens from Water Canyon, 1 mi NE and 1 mi NW Manzano, Torrance Co., is assigned to *S. undulatus tristichus*, but inasmuch as only one of the four adult females has prominent AS, this series too could be regarded as intergradient. Habitat records would be of considerable value in population evaluation where intergradation may be involved, inasmuch as habitat is sharply different among central and southern subspecies of *S. undulatus*.

Intergradation of *S. undulatus belli* with *S. undulatus consobrinus* certainly occurs in northwestern Chihuahua. A specimen (UTEP 3568) from 24 air mi NNE Ascención is an adult male (61 mm SVL) with a spotted dorsum, distinct dorsolateral light lines and separate GS, as in *S. undulatus consobrinus*, but the black borders on the GS are scarcely visible to the naked eye, as in *S. undulatus belli*. Yet a 72 mm SVL male from 9.9 rd mi SW Ascención (UTEP 4271) has the typical unicolor dorsum, dim dorsolateral light stripes and broadly fused GS, as
Table 6. Data on the Four Major Southwestern Subspecies of *Sceloporus undulatus* for all Character-States of Tables 1-5

<table>
<thead>
<tr>
<th>Character-State</th>
<th><em>S. undulatus belli</em></th>
<th><em>S. undulatus consobrinus</em></th>
<th><em>S. undulatus speari</em></th>
<th><em>S. undulatus tristichus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>33(91)</td>
<td>101(73)</td>
<td>48(92)</td>
<td>159(28)</td>
</tr>
<tr>
<td>2</td>
<td>33(85)</td>
<td>150(61)</td>
<td>48(88)</td>
<td>159(18)</td>
</tr>
<tr>
<td>3</td>
<td>33(70)</td>
<td>150(41)</td>
<td>48(85)</td>
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<tr>
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<td>6</td>
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<td>159(52)</td>
<td>65(97)</td>
<td>286(27)</td>
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<tr>
<td>7</td>
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<td>241(56)</td>
<td>65(6)</td>
<td>286(88)</td>
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<td>164(82)</td>
<td>65(43)</td>
<td>295(82)</td>
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<td>171(18)</td>
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<td>168(22)</td>
<td>68(28)</td>
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</tr>
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<td>68(37)</td>
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<td>89(60)</td>
<td>254(74)</td>
<td>68(51)</td>
<td>296(70)</td>
</tr>
</tbody>
</table>

The figures in each column give first the total number of specimens examined for the given character-state, followed parenthetically by the percent of that number having that character-state. See text for the numbered character-states.

in *S. undulatus belli*, to which it is clearly referable (it also has the maximum SVL we have recorded for male *S. undulatus consobrinus*, but within the range - to 74 mm - of male *S. undulatus belli*). Although the locality for *S. undulatus belli* south of Ascención is no more than 50 km from the New Mexico line, that subspecies does not occur in the latter state, to judge from the 83 specimens of the species in the UNM collection from various localities in Hidalgo Co., New Mexico; all are clearly *S. undulatus consobrinus*.

Intergradation of the two subspecies may also occur in in southeastern Chihuahua and southern Coahuila, where their ranges are presumably in broad contact. However, the distinction is sharp between the easternmost sample of *S. undulatus belli* we have seen (UTEP 4459, 6707-8, 6783-5, El Chiflón, 36 km W Saltillo, Hy 40, Coahuila) and the nearest sample of *S. undulatus consobrinus* (UNM 8940-1, 1 mi W and 1 mi S Villa de García, Nuevo León).
Figure 8. Proposed phylogenetic concept of the eleven subspecies of *S. undulatus* currently recognized. The flared base of an arrow indicates apparent existence of intergradation between the connected taxa. No evidence of intergradation of *S. undulatus speari* with other taxa is known but may exist in areas of potential contact as yet not sampled. The names of the taxa and outlines of the ranges of the exerges are so displayed as to reflect approximate geographic position, but length of arrows is not of any significance phylogenetically. The symbol x indicates an isolated population of relictual intergrades between *S. undulatus garmani* and *S. undulatus consobrinus* (cf. Smith et al., 1993).

Rationale

Our continued preoccupation with subspecies is justified in part by the most fundamental purpose of taxonomy: to recognize and provide names for all populational, genetically distinctive "kinds" of organisms. Geographically consistent, genetically distinctive segments of species are also "kinds," just as real as species, and in some cases are more readily distinguished than some species, inasmuch as reproductive isolation, a necessary attribute of species, may be effected without discernible phenotypic effect. On the contrary, the absence of reproductive isolation, an attribute of subspecies, commonly results in readily observed phenotypic differences.
Although the working diagnoses of some of the subspecies of *S. undulatus* have been based on the 70% level of differentiation (Simpson, 1961: 173-176; Mayr, 1969: 188-193), an admittedly arbitrary criterion, *S. undulatus belli* is categorically different from the other subspecies of the *S. undulatus* complex. Hence this is not dealing with a category of convenience (sensu Frost & Hillis 1992), but with a taxon that has an evolutionary history, potentially traceable by phylogenetic-cladistic methods. Figure 8 represents our hypotheses regarding the outcome of such analyses when sufficient data become available to permit their application to the *S. undulatus* complex.

**Acknowledgments**

We are much indebted to the personnel of the various museums from which material has been loaned for our study: Dr Shi-Kuei Wu of UCM; Dr. Arnold Kluge and Greg Schneider of UMMZ; Dr. Howard L. Snell, Dr. William G. Degenhardt (also for zoogeographic counsel) and Allan Landwer, MSB; Ernest A Liner, private collection; and Dr. Robert G. Webb, UTEP (also for habitat information from his field notes on *S. undulatus belli*). Logistic support for field work and facilities for laboratory study were kindly provided by Drs. William M. Lewis, Michael C. Grant and Shi-Kuei Wu of the University of Colorado, and by Dr. Fermín Rivera Agüero of CyMA-UNAM Iztacala; and our collecting permit A00702.-05929 by Dr. Ezequiel Ezcurra of the Instituto de Ecología-SEDESOL. We are especially grateful for the indulgence by Joan, Adam and Laine Chiszar that has been vital for our work on this and related projects, in the field and in the laboratory.

**Literature Cited**


Ferguson, George M. 1982. Distribution, variation and genetic
relationships of the lizard *Sceloporus cautos* Smith in northeastern Mexico. El Paso, Univ. Texas M.S. Diss. xiii, 195 pp., 30 figs.


_____ , _____ , Julio A. Lemos-Espinal & Edwin L. Bell. 1995. The


Appendix

A total of 801 specimens of Sceloporus undulatus was examined during this study. The 69 specimens of S. undulatus speari and all but 85 of the 255 S. undulatus consobrinus are listed in Smith et al. (1994), and are not repeated here; two exceptions (both UTEP) are from 24 air mi NNE Ascencion, Chihuahua (3568), and 30 mi S Monclova, Coahuila (5626), and the remaining 83 (all MSB) are from various localities in Hidalgo County, New Mexico. The 156 S. undulatus belli are cited as types in preceding paragraphs, and the 302 S. undulatus tristichus (all UCM) are as follows.

ARIZONA. Maricopa Co.: Sycamore Creek Campground, nr Sycamore (44030). Pinal Co.: Oak Flat Campground, 4000 ft, 4 mi E Superior (46054-5). Yavapai Co.: 1 mi NW Yarnell (13302, 13305-11); 1 mi W Yarnell (13303-4).

COLORADO. Archuleta Co.: 2 mi N Chromo (7313, 7317, 7320); 2 mi S Chromo (7311-2, 7314-6, 7318-9, 7321, 7323-33, 7335-6); 2 mi S, 0.5 mi W Chimney Rock Peak (51952-3, 52046); 0.5 mi SE Pagosa Springs (5995-6004); 5 mi E Pagosa Springs (52119).

NEW MEXICO. Catron Co.: 2 mi W Aragon (6254); 2 mi E Beaverhead (6314-21); 1 mi E Beaverhead Ranger Station (6304-13); 3 mi NE Horse Springs (6255); 12 mi S Horse Springs, Bat Cave (6286-6303); 1.5 mi SE Horse Springs (6280-3); 1 mi W Horse Springs (2 specimens, unnumbered); 7 mi W Horse Springs (6256); 6 mi WSW Horse Springs (6257-68, 6270-1, 6273-9); nr Old Horse Springs (34140-6). Colfax Co.: 5 mi W Hoxie, Koehler mine (7054, 7062). Harding Co.: 19 mi E Mosquero (13844-7). Mora Co.: Hy 120, 3 mi W Canadian River (13848-60). Rio Arriba Co.: 5 mi E Gallina (7360-8); 2 mi N Regina (7356-9); 9 mi E Youngsville.
(7377-84). Sandoval Co.: Bandolier National Monument Headquarters, 7500 ft (43951-3); 2 mi W Bernalillo (23449-55); 8 mi S Cuba, Hy 44 (10627); 4 mi SW Cuba, Hy 197, 6800 ft (43849-50, 43869-70); 15 mi NW San Ysidro, Hy 44 (10626); Rio Grande 3 mi N Peña Blanca (16820-37, 23219-22, 43896-900, 43905, 43907-9); Rio Grande 3.5 mi N Peña Blanca (43945-7). Sierra Co.: Rito de los Frijoles (73a-c); 18 mi W Winston (6322-36). Taos Co.: 3 mi W Arroyo Hondo, Rio Grande (7011-31); Hy 285, 16 mi S Colorado state line (14692-5); 3.3 mi E Ojo Caliente, 7700 ft (43948-50); Questa (6227); 2.5 mi E Taos (7032-49). Torrance Co.: Water Canyon, 1 mi NE Manzano (23456-7); Water Canyon, 1 mi NW Manzano (23458-62).

UTAH (intergrades, S. undulatus tristichus x S. undulatus elongatus; Smith & Chiszar, 1989). Washington Co.: 4.2-7.2 mi NW Leeds (56061); 25 mi NE St. George (13863-5).
SUMS OF PRODUCTS OF POSITIVE INTEGERS

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Abstract.—Although formulas for, and numerical values of, sums of powers of positive integers appear in any number of handbooks and reference volumes devoted to mathematics, few relationships can be found involving sums of products of positive integers. Included in this paper are a number of formulas for sums of products of two and of three variables. Since sums of products occur frequently, in such diverse fields as combinatorial analysis, numerical approximation of double integrals and complexity of algorithms, these formulas should be useful in a number of applications. Two examples are given illustrating the usefulness of the formulas.

Sums of powers and sums of products of positive integers occur in many combinatorial problems. Although formulas for (Beyer 1970; Selby 1974), and numerical values of (Abramowitz & Segun 1968), sums of powers of positive integers appear in any number of handbooks and reference volumes devoted to mathematics, few relationships can be found involving sums of products of positive integers. Certain of these sums can easily be obtained from the well known formulas for sums of powers of positive integers. For example, to obtain the sum of products of two consecutive positive integers, one has

\[ (1\times2)+(2\times3)+\ldots+((N-1)\times N) = \sum_{i=1}^{N-1} i\times(i+1) \]

\[ = \sum_{i=1}^{N-1} i^2 + \sum_{i=1}^{N-1} i = \frac{N}{3} \times (N-1) \times (N+1) . \]

As another example, consider the sum of products of two consecutive odd positive integers, followed by two even ones, then two odds, and so on, yielding the following:

\[ (1\times3)+(2\times4)+(3\times5)+\ldots+((N-2)\times N) = \sum_{i=1}^{N-2} i\times(i+2) \]

\[ = \sum_{i=1}^{N-2} i^2 + 2\sum_{i=1}^{N-2} i = \frac{(N-2)}{6} \times (N-1) \times (2N+3) . \]
Sums of Products of Two Variables

This paper presents formulas for certain sums of products of two or of three positive integer variables.

Theorem 1

\[ \sum_{1 \leq i,j \leq N} (i \cdot j)^M = \frac{1}{2} \left[ \left( \sum_{1 \leq i \leq N} i^M \right)^2 - \sum_{1 \leq i \leq N} (i^{2M}) \right] \]

Proof: It suffices to show that

\[ 2 \cdot \left[ \sum_{1 \leq i,j \leq N} (i \cdot j)^M \right] + \sum_{1 \leq i \leq N} (i^{2M}) = \left( \sum_{1 \leq i \leq N} i^M \right)^2 = \]

\[ \sum_{i=1}^{N} (i^M) + 2 \sum_{1 \leq i,j \leq N} (i^M \cdot j^M) \]

Corollary 1

\[ \sum_{1 \leq i,j \leq N} (i \cdot j)^M = \frac{1}{2} \left[ \left( \sum_{1 \leq i \leq N} i^M \right)^2 - \sum_{1 \leq i \leq N} (i^{2M}) \right] \]

Proof: Those terms where i=j are added to the result of Theorem 1.

Corollary 2

\[ \sum_{1 \leq i,j \leq N} (i \cdot j) = \frac{N}{24} \cdot (N-1) \cdot (N+1) \cdot (3N+2) \]

Proof: Let M = 1 and use the formulas for the sum from 1 to N of i and i^2, where:

\[ \sum_{i=1}^{N} i = \frac{N}{2} \cdot (N+1) ; \quad \sum_{i=1}^{N} i^2 = \frac{N}{6} \cdot (N+1) \cdot (2N+1) \]

Corollary 3

\[ \sum_{1 \leq i,j \leq N} (i \cdot j) = \frac{N}{24} \cdot (N+1) \cdot (N+2) \cdot (3N+1) \]

Proof: This follows immediately from corollaries 1 and 2.
Corollary 4

\[ \sum_{1 \leq i \leq j \leq N} (i \cdot j)^2 = \frac{N}{12 \times 30} \times (N-1) \times (N+1) \times (2N+1) \times (2N-1) \times (5N+6) \]

Proof: The formulas for the sum from 1 to N of \( i^2 \) and of \( i^4 \) are needed when \( M=2 \), and:

\[ \sum_{i=1}^{N} i^4 = \frac{N}{30} \times (N+1) \times (2N+1) \times (3N^2 + 3N - 1) . \]

Corollary 5

\[ \sum_{1 \leq i \leq j \leq N} (i \cdot j)^3 = \frac{N}{32 \times 21} \times (N-1) \times (N+1) \times (21N^5 + 36N^4 - 21N^3 - 48N^2 + 8) \]

Proof: Sums of cubes and of sixth powers are used, where:

\[ \sum_{i=1}^{N} i^3 = \left[ \frac{N}{2} \times (N+1) \right]^2 ; \sum_{i=1}^{N} i^6 = \frac{N}{42} \times (6N^6 + 21N^5 + 21N^4 - 7N^2 + 1) . \]

Theorem 2

Proof: The recursion equation for the solution \( a_N \) is given by:

\[ a_{N+1} = a_N + (N+1) \sum_{i=1}^{N} i^2 = a_N + \frac{N}{6} \times (N+1)^2 \times (2N+1) . \]

Assuming that \( a_N \) is a fifth degree polynomial in \( N \) (\( a_{N+1} - a_N = 0 \) has zero for a root so the constant coefficient polynomial \( a_N \) must be raised from fourth to fifth power in \( N \)) and solving the finite difference equation for the unknown coefficients, in the same manner that one would solve a linear constant coefficient differential equation with polynomial forcing function (for example refer to Johnsonbaugh 1993), the result follows.

Theorem 3

\[ \sum_{1 \leq i \leq j \leq N} (i \cdot j)^2 = \frac{N}{120} \times (N-1) \times (N+1) \times (12N^2 + 15N + 2) \]
Proof: For this problem the finite recursion equation in $a_N$ is:

$$a_{N+1} = a_N + (N+1)^2 \sum_{i=1}^{N} i = a_N + \frac{1}{2} [N^4 + 3N^3 + 3N^2 + N] .$$

As in Theorem 3, assume that $a_N$ is a fifth degree polynomial in $N$ and solve the resulting difference equation for the unknown coefficients.

**Theorem 4**

$$\sum_{1 \leq i < j \leq N} j \cdot (i+j) = \frac{N^2}{6} \cdot (N-1) \cdot (N+1)^2$$

Proof: Add the results of Theorems 2 and 3.

**Theorem 5**

$$\sum_{1 \leq i < j \leq N} (i^p \cdot j^q) = \sum_{j=2}^{N} \left[ j^q \sum_{i=1}^{j-1} i^p \right] = \sum_{i=1}^{N-1} \left[ i^p \sum_{j=i+1}^{N} j^q \right]$$

Proof: Letting $S_N$ be the value of the summation, by induction it is seen that the equation for recursion, at stage $M$, is given by:

$$S_{M+1} - S_{M} = (M+1)^q \sum_{i=1}^{M} i^p$$ with $S_2 = 1^p + 2^q$.

Iterating for $S_3$, and so on, produces the first of the two double summations. The second double summation is obtained from expanding the first one and then regrouping like terms in $p$.

A Product of Three Variables

**Theorem 6**

$$\sum_{1 \leq i < j < k \leq N} (i \cdot j \cdot k) = \frac{N^2}{48} \cdot (N-2) \cdot (N-1) \cdot (N+1)^2$$

Proof: Note that

$$(1+2+\ldots+N)^3 = \sum_{1 \leq i \leq N} (i^3) + 3 \sum_{1 \leq i \leq N} i^2 \cdot j + 3 \sum_{1 \leq i \leq N} i \cdot j^2 + 6 \sum_{1 \leq i \leq N} i \cdot j \cdot k .$$
The conclusion follows by using the results of Theorems 2 and 3 along with the formulas for the sums of \( i \) and of \( i^3 \) (these formulas appeared in the proofs of Corollaries 2 and 5 of Theorem 1).

**Linear Combinations of Two and Three Variables**

Let \( a \) and \( b \) be any two fixed real numbers.

**Theorem 7**

\[
\sum_{1 \leq i < j \leq N} (ai + bj) = \frac{N(N+1)}{6} * (a+2b) * (N-1)
\]

**Proof:** Letting \( S_N \) denote the summation of the \( ai + bj \) terms, the recursion relationship is given by:

\[
S_N - S_{N-1} = (\sum_{i=1}^{N-1} ai) + Nb * (N-1)
\]

Assuming that the solution for \( S_N \) has the form \( C_1 * N + C_2 * N^2 + C_3 * N^3 \) and using the method of undetermined coefficients, the result follows.

**Corollary**

\[
\sum_{1 \leq i < j \leq N} (ai + bj) = \frac{N(N+1)}{6} * [(a+2b) * (N-1) + 3(a+b)]
\]

**Proof:** Add

\[
\sum_{i=1}^{N} (a + b)i = (a + b) * \sum_{i=1}^{N} i
\]

to the result of the theorem.

**Lemma**

\[
\sum_{N=2}^{N-1} i + \sum_{N=3}^{N-1} i + \ldots + \sum_{N=1}^{N-1} i = \frac{N}{3} *(N-1) *(N-2)
\]
Proof: By expressing
\[
\sum_{N=2}^{N-1} i + \sum_{N=3}^{N-1} i + \cdots + \sum_{N-1}^{N-1} i =
\]
\[
(N-1) + \cdots + 5 + 4 + 3 + 2 +
\]
\[
(N-1) + \cdots + 5 + 4 +
\]
\[
(N-1)
\]
\[
= (N-2)*(N-1) + \cdots + 5*(4) + 4*(3) + 3*(2) + 2*(1)
\]
it is clear that this is the same as (except for one term less) the first relationship given in the introduction, thus giving the desired result.

Theorem 8
\[
\sum_{1 \leq i < j < k \leq N} (ai + bj + ck) = \frac{N}{24}*(a+2b+3c)\times(N-2)\times(N-1)\times(N+1)
\]
the recursion relationship is given by:
\[
S_N - S_{N-1} = b[\sum_{N=2}^{N-1} i + \sum_{N=3}^{N-1} i + \cdots + \sum_{N-1}^{N-1} i] +
\]
\[
a[1(N-2) + 2(N-3) + \cdots + (N-2)(1)] + Nc[(N-2) + (N-3) + \cdots + 1]
\]
which by the lemma becomes
\[
b[\frac{N}{3} \times(N-1)\times(N-2)] + a \sum_{i=1}^{N-2} i\times(N-i-1) + cN \sum_{i=1}^{N-2} i
\]
and this simplifies down to
\[
\frac{(a+2b+3c)}{6} \times N\times(N-1)\times(N-2)
\]
Assuming that \( S_N = (C_1 N^3 + C_2 N^2 + C_3 N + C_4 ) \times N \), substituting into the recursion equation and solving for the \( C_i \) terms gives the desired result.
Conclusions

Two examples illustrating the usefulness of the formulas are now presented, one from combinatorics and the other from the field of numerical approximations.

Given a fixed positive integer \( N \) greater than 1; on each day \( i \), from day 1 through day \( N-1 \), choose 1 man from a group of \( i \) men and choose 1 woman from a group of at least \( i+1 \), but no more than \( N \), women. Then \( \sum ij \), where \( 1 \leq i < j \leq N \), gives the total number of possible selections made during the \( N-1 \) days. This value can then be found using the formula given in Corollary 2 to Theorem 1.

A method for approximating the value of the double integral

\[
\int_{0}^{1} \int_{0}^{y} (x^2 + y) \, dx \, dy
\]

is to divide \([0,1]\), along both the x- and the y-axes, into subintervals of length \( \Delta x = \frac{1}{N} = \Delta y \). Then, using the \((i/N,j/N)\) endpoint in each square area \([((i-1)/N,i/N)\) by \([((j-1)/N,j/N)\) to calculate \( f(x,y) = x^2 y \),

\[
(\Delta x)(\Delta y) \sum_{1 \leq i < j \leq N} \left( \frac{i}{N} \right)^2 \left( \frac{j}{N} \right) = \frac{1}{N^5} \sum i^2 j
\]

approximates the value of the double integral. Using the formula in Theorem 2, with \( N \) being a mere 4, gives an approximation of .071289, only 0.46 of 1% from the actual value of 0.066666.

Literature Cited


GROWTH MODELS OF LOBLOLLY PINE FROM EAST TEXAS AND LOST PINES SEED SOURCES GROWING IN THE POST OAK BELT OF TEXAS

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Abstract.—A total of 92 loblolly pines from 32 old-field pine plantations located in the Post Oak Belt of east Texas were examined to determine growth differences of trees grown from different seed sources. Results indicate that trees from East Texas seed sources exhibited greater height growth than those from Lost Pines seed sources.

The Post Oak Belt of East Texas is an area of transition between the pine forest to the east and the prairies to the west. This area extends from the Red River southward, contiguous with the western edge of the pine forest and extending into Central Texas. The forests of this zone are dominated by post oak (Quercus stellata Wang.) and blackjack oak (Q. marilandica Muenchh.) in association with other dry site oaks, hickories (Carya spp.), and elms (Ulmus spp.) (cf. Tharp 1939; Duabenmire 1978; Diamond et al. 1987). Pine occurs naturally in some areas of this zone. Loblolly pine (Pinus taeda L.) occurs in Bastrop, Caldwell, and Fayette counties (Tharp 1939). This area is known as the Lost Pines because it is separated from the contiguous range of loblolly pine to the east. Shortleaf pine (P. echinata Mill.) occurs in isolated natural stands (Wilson & Hacker 1986; Wilson 1989) further to the north in Lamar and Franklin counties.

The possibility of growing pine in some areas of the Post Oak Belt has been postulated (Bray 1904; Walker 1972). Indeed, since 1930 many pine plantations were established from both East Texas seed sources as well as the Lost Pines seed source which is cultivated as drought hardy planting stock. The purpose of this study was to quantify height growth for loblolly pine from East Texas and Lost Pines seed sources growing on old-field sites in the Post Oak Belt.
Table 1. Loblolly pine regression coefficients for Lost Pines vs. East Texas seed sources

<table>
<thead>
<tr>
<th>Type</th>
<th>(b_1)</th>
<th>(b_2)</th>
<th>(b_3)</th>
<th>(r^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Sites Combined</td>
<td>99.147</td>
<td>.057</td>
<td>1.560</td>
<td>.9078</td>
</tr>
<tr>
<td>East Texas</td>
<td>106.351</td>
<td>.054</td>
<td>1.558</td>
<td>.9305</td>
</tr>
<tr>
<td>Lost Pines</td>
<td>70.861</td>
<td>.058</td>
<td>1.353</td>
<td>.9292</td>
</tr>
</tbody>
</table>

Methods and Materials

Data for this study came from 32 old-field plantations in the Post Oak Belt of East Texas. Of these, 25 (78%) were from the East Texas Seed source and seven (22%) were from Lost Pines Seed source. Ages of the plantations ranged from 12 to 46 years. Heights ranged from 22.75 ft (6.93 m) to 98.67 ft (30.07 m) with diameters ranging from 5.4 in. (13.7 cm) to 15.2 in. (38.6 cm).

Sampling was done by approximating the center of each plantation and felling one to three dominant or co-dominant trees per plantation. Only typical, single-stemmed individuals which were free of suppression were selected. Only one tree per plantation was sampled in some cases due to land owner restrictions. Ninety-two trees were sampled.

Examination of the individual sample trees was conducted by felling and then deliming to the terminal leader. Cross-sectional cuts were then made at 24-inch (61 cm) intervals and the rings at the top of each bolt counted and recorded. The 92 stem analysis trees yielded 1707 height-age pairs, of which 1404 were from the East Texas seed source and 303 were from the Lost Pines seed source. True heights were estimated using the adjustment recommended by Carmean (1972).

A height-growth model using the Chapman-Richards (1959; 1961) function:

\[ Y = b_1[1.0-\exp(b_2*\text{Age})]^b_3 \]

Where: \(Y\) = Tree Height (feet), and \(b_1, b_2, b_3\) = Parameters to be determined

produced an excellent fit \((r^2 = .9078)\) when applied to the entire data set. A plot of residuals showed no adverse biases or trends. The same method was applied individually to the data for each seed source. Regression coefficients, standard errors, and \(r^2\)'s for all regressions are shown in Table 1.
Results and Discussion

After inserting the regression coefficients from Table 1 into the Chapman-Richards function, the following equations resulted:

\[
\text{East Texas seed source:} \quad \text{Height} = 106.351[1.0-\exp(-0.054*\text{Age})]^{1.560} \tag{2}
\]

\[
\text{Lost Pines seed source:} \quad \text{Height} = 70.861[1.0-\exp(-0.058*\text{Age})]^{1.353} \tag{3}
\]

When plotted, these models display curves (Figure 1) indicating that for loblolly pine growing in the Post Oak Belt, trees from East Texas seed sources exhibit greater height growth than those from Lost Pines seed sources.

The difference in observed height growth patterns is understandable as loblolly pine from the Lost Pines area has fewer rows of stomata, fewer stomata per row, and consequently fewer total stomata (Knauf & Bilan 1972; 1977). Stomata of the Lost Pines loblolly pine close more readily with the onset of drought than do those of the East Texas seed sources (Bilan et al. 1977). These adaptations to drought could possibly limit photosynthesis, hence limit growth. Differences noted here in height growth patterns of the Lost Pines and East Texas loblolly pine growing in the Post Oak Belt may not be applicable for other areas.
Literature Cited


HYBRIDIZATION AMONG MEMBERS OF THE GENUS MORONE (PISCES: PERCICHTHYIDAE) IN GALVESTON BAY, TEXAS

Rocky Ward, Ivonne R. Blandon and Britt W. Bumguardner
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Abstract.—Based upon isoelectric focusing, this study reports the natural occurrence of a Morone saxatilis x M. mississippiensis hybrid as well as an individual specimen which is interpreted to be the product of a hybrid (probably M. chrysops x M. saxatilis) crossing with a member of a third species (M. mississippiensis).

Hybridization in the genus Morone has been well documented. Artificial production of both M. saxatilis x M. chrysops hybrids (Stevens 1965; Bishop 1967) and M. saxatilis x M. mississippiensis hybrids (Ware 1975; Harvey & Fries 1985) has been described. Under natural conditions M. saxatilis x M. chrysops hybrids have been reported along with individuals interpreted to be F₂ hybrids and/or backcrosses (Avise & Van Den Avyle 1984; Forshage et al. 1986). Morone chrysops x M. mississippiensis hybrids have been collected under natural conditions (Harvey & Fries 1987; Fries & Harvey 1989) but have not been shown to reproduce. This report describes the use of isoelectric focusing (IEF) to document the natural occurrence of a M. saxatilis x M. mississippiensis hybrid and an individual which is interpreted to be the offspring of a hybrid (probably M. chrysops x M. saxatilis) mating with a member of a third species (M. mississippiensis).

Methods and Materials

Muscle tissue samples were obtained from specimens collected in Galveston Bay near the Houston Lighting and Power Company’s Cedar Bayou Plant cooling lake spillway by Texas Parks and Wildlife Department (TPWD) personnel during the spring of 1993. Tissue samples were refrigerated in transit to the Perry R. Bass Marine Fisheries Research Station where they were stored at -85°C until processed. Tissue samples were individually homogenized in an equal volume of distilled water and centrifuged at 10,000 rpm for 10 minutes at 4°C. The resulting supernatant was retained for analysis and maintained at -85°C.

Isoelectric focusing was conducted on 0.25 mm polyacrylamide gels consisting of 2 ml 29.1 % (wt/vol) acrylamide and 0.9 % N,N'-methy-
lenebisacrylamide, 1.0 ml ampholytes (pH gradient 4-5; Crescent Chemical, Hauppa, NY), 4.2 ml deionized water, and 1.0 ml glycerol. Procedures for conducting IEF and for visualization of sarcoplasmic proteins follow those described by King et al. (1991).

Gels were scanned to determine protein migration and absorbance (intensity) utilizing an Ultrascan XL Laser Densitometer loaded with LKB Gelscan 2.0 software (Pharmacia LKB Instruments, Gaithersburg, MD). Isoelectric points (pis) were assigned to resulting bands based on comparison with pi values of bands produced by commercial protein markers (Sigma Biochemicals, St. Louis, MO).

Results

Densitometric tracings of banding patterns are shown in Figure 1 for *M. chrysops*, *M. mississippiensis*, *M. saxatilis*, a *M. saxatilis* x *M. mississippiensis* hybrid, and a tracing with bands interpreted to represent a complex hybrid characterized by bands derived from each of the three species of *Morone*. *Morone chrysops* (Figure 1a) has a band at pi 4.53 which distinguishes it from its congeners, and lacks a band at pi 4.03 which is present in the other two species. *Morone mississippiensis* (Figure 1b) has a diagnostic band at pi 4.30. *Morone saxatilis* (Figure 1c) has a diagnostic band at pi 4.86 and lacks a band at pi 4.07 which is present in congenerics. The *M. saxatilis* x *M. mississippiensis* hybrid (Figure 1d) has a band corresponding to each of the major bands of the parental species, though, as expected, the intensity of the bands are reduced relative to those found in the parentals.

The pattern in Figure 1e represents an individual interpreted to be the offspring of a *M. chrysops* x *M. saxatilis* hybrid which mated with a *M. mississippiensis*. In the offspring of a mating of this type one expects to find all bands of the P₂ non-hybrid species (*M. mississippiensis*) expressed and, on the average, 50% of the unique bands of the two P₁ species expressed. This individual expresses the diagnostic band of *M. saxatilis* at pi 4.86, the diagnostic band of *M. mississippiensis* at pi 4.30, and the diagnostic band of *M. chrysops* at pi 4.53. Lacking is the band diagnostic of *M. chrysops* at pi 4.07 suggesting that *M. chrysops* is a P₁ parental species.

It should be noted that the observed protein patterns would support the hypothesis that the individual resulted from a *M. chrysops* x *M. mississippiensis* hybrid crossing with *M. saxatilis*. However, because of intense stockings of *M. chrysops* x *M. saxatilis* hybrids by TPWD, it is more likely that the parental hybrid was of the latter type.
Figure 1. Densitometric tracings and isoelectric points for representative sarcoplasmic protein bands of three species of *Morone* found in Galveston Bay and two suspected hybrid individuals subjected to isoelectric focusing in a pH 4-5 gradient. Migration distance is relative to the anodal (+) electrode strip.

**Discussion**

The only hybrid *Morone* stocked by the TPWD are the *M. chrysops* × *M. saxatilis* crosses. Therefore, the two hybrid fish described in this report almost certainly represent natural occurrences. Finding that hybrid *Morone* will mate with a different member of the complex is not surprising. The isolating mechanisms within this genus do not appear strong; once a hybrid is produced those mechanisms may be weakened further.

Fries & Harvey (1989) expressed concern about use of incorrectly identified (hybrid) *Morone* as broodfish in enhancement programs and the deleterious effects stocking their backcross offspring could have on the genetic integrity of resident populations. This concern is reinforced by the discovery of complex hybridization in the present study.

Well conceived stocking programs have the potential to enhance a fishery while producing little or no negative impact on natural
populations. However, when members of a closely related taxon are present in a drainage, stocking should be attempted only after careful consideration is given to potential negative impacts.

Acknowledgements

Robert L. Colura, Lawrence W. McEachron and Lorraine T. Fries provided useful criticism of this manuscript.

Literature Cited


GENERAL NOTE

AN ADDITIONAL RECORD OF THE NATIVE AMERICAN ELK (CERVUS ELAPHUS) FROM NORTH TEXAS

Brian S. Shaffer, Bonnie C. Yates and Barry W. Baker
Zooarchaeology Laboratory, Institute of Applied Sciences, University of North Texas, Denton, Texas 76203-6078; United States Fish and Wildlife Service, Forensics Laboratory, Ashland, Oregon 97520; and Department of Anthropology, Texas A&M University, College Station, Texas 77843-4352

Pfau (1994) reported the first record of physical evidence of the native elk (Cervus elaphus) from Texas. He noted the recovery of the distal end of a tibia of an adult individual from Baylor County in central north Texas. The specimen was radiocarbon dated at 295 (± 50) YBP. This note is to bring attention to the report of a second elk specimen from northern Texas. Shaffer (1994) cited the recovery of a proximal phalange of an elk from an Early Caddo Indian archaeological site (41DT11) in Delta County in northeast Texas. The specimen was recovered from a garbage midden (Lot 191, Unit 15, Level 5). The midden was dated at 520 to 980 YBP based on six calibrated (1-sigma) radiocarbon samples (Fields & Gadus 1994).

The phalange is nearly complete, with slight fragmentation on the proximal end. The proximal epiphysis was in the process of fusing at the time of death of the animal. Using criteria established by Brown & Gustafson (1989), the specimen was identified based upon comparison of skeletal material available at the Zooarchaeology Laboratory of the Institute of Applied Sciences at the University of North Texas. Identification was verified by the U.S. Fish and Wildlife Service Forensics Laboratory in Ashland, Oregon. The specimen is housed with other materials from archaeological site 41DT11 at the Texas Archeological Research Laboratory, J. J. Pickle Research Campus, University of Texas at Austin.

Pfau (1994) noted that it was unclear as to whether the Baylor County specimen was from a substantial elk population or that of a single wandering individual. This additional find, combined with the infrequency of elk finds in Texas, appears to support Pfau’s hypothesis that the American Elk was only an occasional transient into northern Texas.
Acknowledgements

We wish to thank Karen M. Gardner, George Baumgardner, and Prewitt and Associates, Inc. of Austin for their help with this project. Our appreciation is extended to Darrell Creel of the Texas Archeological Research Laboratory for his assistance and to two anonymous reviewers for their comments.

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PROXIMITY OF STREAMS TO LANDFILLS
IN NORTH-CENTRAL TEXAS

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Abstract.—A geographic information system was used to identify segments of the upper Trinity River drainage network that are within various distance thresholds of solid waste landfills. U.S. Geological Survey digital line graph (DLG) data were used to create a hydrography coverage for the study area. Landfill coordinates were obtained from a database maintained by the Texas Natural Resource Conservation Commission. At a map scale of 1:100,000, 54 km (0.42%) of the drainage network are located within 100 m of at least one landfill and 25 km of these stream segments are upstream of water supply reservoirs. The approach employed herein can prioritize local hydrogeologic investigations and facilitate strategic environmental monitoring to indicate potential landfill-derived contamination of surface water resources.

Leachates derived from landfills can migrate within shallow groundwater flow systems that discharge into streams. This process is referred to as base flow contamination. Groundwater monitoring can identify the presence of landfill-derived contaminants, thereby facilitating remedial action to prevent stream pollution. However, it is not economically feasible to rigorously monitor an entire drainage basin. A more cost-effective approach is to prioritize monitoring activities by systematically identifying high-risk segments of a drainage network.

The hazard that a landfill poses to a surface water body depends on several factors including: (1) the distance between the landfill and surface water; (2) the hydrogeologic characteristics of rock units between the landfill and surface water; and (3) the configuration of the water table downslope of the landfill.

The objective of this study was to evaluate the proximity of streams to landfills using a geographic information system. An application was developed that systematically identifies segments of a drainage network within specified distances of waste storage facilities such as landfills. The approach was applied to the Upper Trinity River drainage basin in north-central Texas (Figure 1).

Prior Investigations

Mapping and analytical capabilities of geographic information systems (GIS) have been used in a variety of hydrologic applications (DeVantier
A common GIS application is defining spatially distributed input parameters for hydrologic models. Model output can be studied to evaluate the impact of land use practices on water quality in streams or aquifers. Surface water applications include flood plain management (Davis 1978), nonpoint pollution modeling (Tim et al. 1992), and urban runoff modeling (Shea et al. 1993).

Geographic information systems also have been linked with groundwater models to delineate protection areas for public water supply wells (Griner 1993). Hudak et al. (1993) demonstrated an application of GIS to designing groundwater monitoring networks near a solid waste landfill. Several studies have used GIS to derive maps showing vulnerability of groundwater to pollution (e.g., Evans & Meyers 1990; Griner 1993). These studies employed GIS capabilities for overlaying multiple information layers to derive composite indices of groundwater pollution potential.

Another important GIS application in water resource management is identifying locations of potential contamination sources. Richards (1993) georeferenced a database of waste facilities discharging effluent in Louisiana. Hunt et al. (1993) used a GIS approach to inventory contaminant sources overlying the Spokane Aquifer in Washington. These inventory studies employed mapping capabilities of GIS, but did not involve a spatial analysis to evaluate contamination hazard. This study demonstrates the analytical capabilities of GIS for evaluating
spatial relationships between streams and landfills. The approach systematically identifies segments of a drainage basin that may be at risk of base flow contamination because of their proximity to waste storage facilities.

Study Area

The study area is the upper Trinity River drainage basin in north-central Texas (Figure 1). Its outlet is at the confluence of the East Fork and main branch of the Trinity River. The population of the study area is about 3.9 million (Ulery et al. 1993). Due to a large urban population, municipal water is by far the largest basin demand (about 75% of total in-basin demands). Other major water demands include manufacturing (9%), irrigation (6%) and steam electric power generation (6%) (Texas Water Development Board, 1993). Water demands are most rapidly growing for municipal and manufacturing purposes.

Surface water is the primary source of municipal water in north-central Texas. The Texas Water Development Board (1993) projects that the region’s reliance on surface water relative to groundwater will increase with time. The U.S. Geological Survey has identified solid waste landfills in the vicinity of streams as a significant water quality issue in the Trinity River basin (Land 1991). The first step taken to address this problem was to evaluate the spatial distribution of stream reaches that comprise the drainage network in relation to the numerous landfills in the area.

Methodology

The UNIX version (6.1) of ARC/INFO (ESRI 1992) was the GIS software used for the study. The computing platform was a PC 486-50 running X Windows emulation software. A hydrography coverage (streams and lake boundaries) was constructed from digital line graph (DLG) files stored on compact disk, obtained from the U.S. Geological Survey (USGS). Disk 8, which covers Texas and Oklahoma, was used in this study. DLG’s are digital representations of points, lines and areas of planimetric information. This study used DLG’s derived from 30-minute by 60-minute, 1:100,000 scale USGS quadrangle maps. Digital data are encoded to express the spatial relationships that exist between map elements. Features were registered to the Universal Transverse Mercator (UTM) coordinate system.

After extracting the DLG’s for ten quadrangles that contained the
study area, ARC/INFO's CLEAN and MAPJOIN commands were used to create a topologically structured hydrography layer. Using the hydrography coverage as a back coverage in the ARCEDIT module, the basin divide for the study area was digitized, thereby generating a basin divide layer. This coverage was used to clip out the relevant section from the hydrography coverage. This clipped hydrography coverage was used in conjunction with a landfill coverage to perform proximity analyses.

A landfill coverage was generated from the Permit Application Database maintained by the Texas Water Commission (now the Texas Natural Resource Conservation Commission). Distributed on computer diskette, this dBASE file contains data for permitted and known unauthorized landfill sites in Texas. For each permitted site, the database lists its number along with associated characteristics (attributes). Illegal sites are not assigned an actual permit number, but receive an identification number. The attributes used in this study were county code, geographic coordinates (latitude and longitude), facility size (acres), and facility type.

Most facilities in the database are municipal sanitary landfills. However, the database also catalogues sanitary landfills for brush and/or construction-demolition material, transfer stations, waste incinerators and other waste processors, sludge disposal sites, and tire storage sites.
County codes were used to identify facilities within or near the study area. (Some counties straddle the perimeter of the study area.) Latitude and longitude coordinates were projected to UTM coordinates, and the basin divide coverage was used to clip out a point coverage of landfills within the study area.

The landfill and hydrography coverages were used to identify segments of the drainage network within specified distances of at least one landfill. Points representing landfills were buffered according to the area of the landfill and a distance (proximity) threshold. A graphical depiction of the actual boundaries of the numerous landfills was not available. Boundaries of inactive landfills have been obscured by other land uses.

The buffer zone employed approximates the area within a proximity threshold of a landfill. It was derived by taking the sum of two smaller buffers, one defining the perimeter of a circle with an area equal to that of the landfill, and the other equal to a specified proximity threshold. Although alternative geometric shapes could be used to represent the areal extent of a landfill, the circle was selected because it does not impose any directional bias from the reported latitude-longitude coordinate pair.
Figure 4. Stream segments within 1,000 m (top), 500 m (middle), and 100 m (bottom) of at least one landfill.
For a landfill with acreage $A_a$, the equivalent area in square meters is

$$ A_m = 4,049A_a $$

(1)

The radius of a circle with an area $A_m$ is

$$ R_m = \left(\frac{A_m}{3.14}\right)^{1/2} $$

(2)

Adding a proximity threshold $P_m$ to $R_m$ gives the total buffer $T_m$ for a landfill with area $A_a$ (subscripts $a$ and $m$ designate distance units of acres and meters, respectively):

$$ T_m = (1,290A_a)^{1/2} + P_m $$

(3)

For a specified proximity threshold, equation (3) was used to define appropriate buffers for each point in the landfill coverage. The buffered landfill coverage was used to clip the hydrography coverage, thereby generating a new coverage of stream segments within the specified proximity threshold, $P_m$, of at least one landfill. Proximity thresholds of 1,000 m, 500 m, and 100 m were analyzed in the study. The thresholds were chosen to provide a range of distance values corresponding to different levels of contamination hazard.

In the final phase of the study, the part of the study area that was upstream of one or more water supply reservoirs was defined. The perimeter of the upstream area was digitized in the ARCEDIT module, using the hydrography and basin divide coverages as background layers. The resulting upstream polygon was used to clip each of the three stream segment coverages generated in the preceding analysis. Thus, the final set of maps showed the stream segments that were within a proximity threshold of at least one landfill and upstream of one or more water supply reservoirs. Cumulative lengths of stream segments in the various coverages were calculated from corresponding arc attribute tables (using the STAT command in the TABLES module).

Results

A total of 165 facilities comprise the landfill coverage (Figure 2). Many of the landfills are located near major tributaries of the Trinity
Figure 5. Stream segments within 1,000 m (top), 500 m (middle), and 100 m (bottom) of at least one landfill and upstream of a water supply reservoir (facility identification numbers are shown in detailed area map).
River drainage network. The areas of the landfills range from approximately 0.04 ha to 391 ha. In general, the larger landfills occupy the more heavily populated southern half of the study area (Figure 3). Figure 3 was generated with ARC/INFO’s ERASE command, by overlaying coverages for progressively smaller landfill size categories. The circle sizes were selected to provide visual contrast between landfill area categories. (Smaller landfills are not actually located inside of larger landfills.)

The total length of all streams comprising the hydrography coverage for the study area is 12,850 km. Respectively, 434 km (3.4%), 194 km (1.5%), and 54 km (0.42%) of the drainage network are within 1,000 m, 500 m, and 100 m of at least one landfill (Figure 4).

The preceding results identify segments of the drainage network that are close to landfills, but do not account for the locations of water supply reservoirs. Respectively, 224 km, 98 km, and 25 km of the drainage network are within 1,000 m, 500 m, and 100 m of at least one landfill and upstream of a water supply reservoir (Figure 5). Many of these stream reaches may warrant local hydrogeologic investigations to evaluate the hazard of base flow contamination. Detailed windows in Figure 5 show stream segments within a proximity threshold in relation to other segments of the drainage network.

Summary and Conclusions

There are many landfills near streams comprising the upper Trinity River drainage network. Relatively inexpensive land may have been an economic incentive for locating waste disposal sites in flood plain deposits. While economically advantageous, these landfills can potentially contaminate shallow groundwater which discharges to streams. Streams supply several surface water reservoirs in north-central Texas.

One of the factors that dictates base flow contamination hazard is the proximity of a stream to waste storage facilities. Using geographic information systems, the study identified segments of the upper Trinity River drainage network that may warrant local hydrogeologic investigations based on their proximity to landfills. Buffering and map overlay operations were particularly useful in conducting the analysis. At a map scale of 1:100,000, 54 kilometers of the drainage network are within 100 meters of at least one landfill. Twenty-five km of those stream segments are located upstream of water supply reservoirs.
Results of a proximity analysis such as that conducted herein can prioritize site specific investigations and environmental monitoring activity. Drilling and surface geophysics are examples of tools that can be used to characterize deposits between landfills and streams. Stream reaches that are relatively close to landfills warrant the monitoring of (1) groundwater between the landfill and stream reach, and (2) surface water within the stream reach.

Acknowledgments

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on geographic information systems and water resources, American Water Resources Association.


THE PSITTACIDS (AVES: PSITTACIDAE) OF EL BAGUAL ECOLOGICAL RESERVE OF NORTHEASTERN ARGENTINA

A. Alberto Yanosky and Claudia Mercoll

Abstract.—El Bagual Ecological Reserve in northeastern Argentina exhibits a psittacid fauna composed of eight species. These include five species of parakeets, two parrots and one parrotlet. Seasonal occurrence and habitat preference based upon a two year study is reported for each species.

Resumen.—La Reserva Ecológica El Bagual: ubicada en el noreste la provincia de Formosa, Argentina. Posee una fauna de psittádidos compuesta por ocho especies. Se informa para cada especie la estacionalidad en orden de importancia, y la preferencia de hábitat basada en dos años de estudio.

The natural environment of the Chaco region of Argentina is undergoing extensive alteration due to intensive deforestation and agricultural practices. Dabbene (1935) examined the psittacids of this region based upon their potential damage to crops. He also noted the need of managing some wild psittacid populations. Many of the members of this family are among the most solicited and highest priced pets in the world market (Perez & Equiarte 1989). The trade with these species can be traced back to 1816, when in Georgetown, Guyana, aboriginals traded psittacids with the Europeans (Waterton 1825).

Contreras (1987) includes 12 species of psittacids among the avifauna of the state of Formosa in northeastern Argentina. Two species are considered of doubtful occurrence within the state. Of the remaining 10 species, eight occur within the boundaries of El Bagual Ecological Reserve. Four of these were listed by Dabbene (1935) as problem species. This study was undertaken to provide base-line information relative to seasonal occurrence and habitat preference for the eight species of psittacids occurring within the non-agricultural and protected habitat of the reserve.

Study Area

El Bagual Ecological Reserve was established in 1985 to provide an area of protected habitat north of the Río Bermejo lowlands in the east-
ern part of the state of Formosa, Argentina. It covers an area of approximately 35 km² in the Humid Chaco biogeographical region and is characterized by areas of grasslands and forests. The region is subjected to naturally occurring floods and fires (Morello & Adamoli 1974). For the purposes of this study, the reserve can be divided into the following four general ecological zones or areas based upon differences in vegetational types.

Grasslands.—These are lowland areas which were formerly used for agricultural purposes and are now abandoned. This area includes the "bañados" which are flooded most of the year and exhibit poorly defined borders with their adjacent grasslands.

Low shrub.—This type of habitat borders the lowlands and is characterized by low shrub. Depending upon elevation, this area may or may not be subjected to flooding.

Low forest.—This habitat area is characterized by the presence of woody trees which attain heights of 15 to 17 m.

Upper forest.—This type of habitat is characterized by the presence of woody trees which exhibit upper stratifications and attain heights in excess of 20 m.

Methods

Following the methods of Emlen (1971), 189 transect censuses were conducted for each season of the year from May of 1987 through April of 1989. Transects in dense forest were 100 m by 30 m and in open areas 1000 m by 300 m. All censuses were conducted during early morning hours on cloudless days. The results were used to determine seasonal occurrence and habitat preference for each species of psittacid inhabiting the reserve.

Results

The following species accounts represent the results of the two year survey at El Bagual. They are ranked in order of their relative occurrence within the reserve; the first species is the most common and the last is least common. Common names follow those of Narosky & Yzurieta (1987).
Myiopsitta monachus (Boddaert)
(Monk Parakeet)

Occurrence.—This is the most common species of psittacid observed within the reserve. While present throughout the year, numbers of individuals peak during the spring months. This species was observed to nest within the reserve.

Habitat.—Except for the high forest, it was observed in all other habitats throughout the year. It is most frequently encountered in low shrub and areas near the bañados.

Pyrrhura frontalis (Vieillot)
(Reddish-bellied Parakeet)

Occurrence.—While most common during the fall, this species of parakeet is present within the reserve throughout the year. It also nests within the reserve.

Habitat.—It is most commonly encountered in the low and upper forested areas.

Nandayus nenday (Vieillot)
(Black-hooded Parakeet)

Occurrence.—While most common during the winter months, this species is present within the reserve throughout the year. This species also nests within the boundaries of the reserve.

Habitat.—It is commonly encountered from the low shrub to the upper forest areas. Open areas are used as transitory routes by this species.

Amazona aestiva (Linnaeus)
(Turquoise-fronted Parrot)

Occurrence.—This species is present within the reserve throughout the year. It nests within the boundaries of the reserve.

Habitat.—While observed in all habitat types, it is more frequently encountered in the lower and upper forest areas. Open areas are infrequently used as transitory routes.

Remarks.—This parrot is the largest species of psittacid occurring within the reserve. Due to hunting pressures upon wild populations, this
species is considered threatened by the Wildlife National Bureau (Balabusic et al. 1990).

*Pionus maximiliani* (Kuhl)
(Scaly-headed Parrot)

**Occurrence.**—This parrot was observed within the reserve only during the winter months. This species was not observed to nest within the reserve.

**Habitat.**—During winter months it was noted to be present in relatively high numbers in the low shrub areas of the reserve.

*Aratinga acuticaudata* (Vieillot)
(Blue-crowned Parakeet)

**Occurrence.**—This species is found within the reserve from spring to fall; it was not observed to be present during the winter months. It nests within the boundaries of the reserve.

**Habitat.**—While observed transitory in other areas of the reserve, it exhibits a preference for the uppermost strata of the upper forest areas.

*Aratinga leucophthalmus* (Müller)
(White-eyed Parakeet)

**Occurrence.**—This species is most commonly observed during the spring and summer months. It is not present during the winter and is only transitory during the autumn. This species does nest within the boundaries of the reserve.

**Habitat.**—While this species may occur from the low shrub to the upper forest areas, it is most often observed in the upper forest.

*Forpus xanthopterygius* (Spix)
(Blue-winged Parrotlet)

**Occurrence.**—During the course of the two year study, this species was observed on only two occasions during summer months. The reserve borders upon the south-western limit of the range of this species. It is considered rare at El Bagual.

**Habitat.**—When observed, it was in the upper forest.
Acknowledgements

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HABITAT USE BY WINTERING SHOREBIRDS ALONG THE LOWER LAGUNA MADRE OF SOUTH TEXAS

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Abstract.—Censuses of wintering shorebirds were conducted in mudflat habitats along the lower Laguna Madre during November-February of 1992-1993 and 1993-1994. Widespread species such as Western Sandpipers (Calidris mauri), Willet (Catoptrophorus semipalmatus), Black-bellied Plovers (Pluvialis squatarola), and dowitchers (Limnodromus spp.) used both high and low mudflats, peaking during low water conditions. Long-billed Curlews (Numenius americanus) and Marbled Godwits (Limosa fedoa) used mainly low mudflats, while American Avocets (Recurvirostra americana) and Stilt Sandpipers (Calidris himantopus) were restricted to pools on the high mudflats. Piping Plovers (Charadrius melodus), Snowy Plovers (Charadrius alexandrinus) and other small Charadrius plovers were uncommon, occurring mainly on high mudflats and algal flats before these were covered with glasswort (Salicornia bigelovii).

The lower Laguna Madre, which is located in subtropical southern Texas, is characterized by extensive unvegetated mudflats and sandflats near mean sea level as well as large areas covered by seagrasses below mean sea level (Britton & Morton 1989). Mild winters and extensive intertidal flats support the existence of many shorebirds in the Laguna Madre region of both Texas and Tamaulipas (Mitchell & Boyd 1992; Morrison et al. 1993; Withers & Chapman 1993). Some of the largest known wintering populations of the threatened Piping Plover and the declining Snowy Plover also occur in the Laguna Madre of south Texas (Haig & Plissner 1993). This study was undertaken to determine patterns of habitat use by shorebirds and their responses to changing habitat conditions during winter months along the lower Laguna Madre of south Texas.

Study Areas

All study areas were located along the western shore of the lower Laguna Madre, Cameron Co., Texas, 26°04'-26°22'N and 97°10'-97°20' W. Habitats were classified based on frequency of exposure and presence of pools, algal flats, or seagrass. Large areas of intertidal habitat are alternately exposed and covered by wind shifts associated with fronts during the winter (Mitchell 1992), whereas the effects of astronomic tides are restricted to passes (Breuer 1962).
High Mudflat/Pool.—This area is comprised of a large complex of enclosed shallow water and exposed, firm mudflat just west of Horse Island in Unit 5, Laguna Atascosa National Wildlife Refuge (LANWR). This is the only plot to have a relatively permanent, shallow pool, which covered the deepest portion of the study area. Strong south and southeast winds exposed extensive mudflats ≥2000m wide, whereas north and northwest winds exposed more limited areas of mudflats. Blue-green algae formed isolated mats over the mud in areas periodically exposed, but such algal mats were poorly developed and temporary. Although nearly devoid of vegetation in November 1992, some of the mudflats within 50 m of the usual water’s edge became partially covered with glasswort (*Salicornia bigelovii*) during December-February 1992-1993. By November 1993, glasswort covered large areas of secondary coves and other regularly-inundated sites throughout the study area.

High Algal Flat.—This area is located immediately south and east of Horse Island and is characterized by wind-tidal flats covered with a well-developed algal mat. The algal mat provided a firm, tough surface in much of this study area. High Algal Flat was covered with water during strong southeast winds or seasonal high water, and was exposed by strong north and northwest winds. Limited *Salicornia* covered this flat by February 1993, but coverage never became dense in this area. There was no increase in glasswort density during the second winter, but dead glasswort stalks remained on the flats during the second winter. New germination was not noticed until late February 1994.

Low Mudflat.—This area (the shoreline section of Bayside Tour Loop, Unit 7, LANWR) includes the shoreline and associated mudflat and seagrass areas visible from the shore. These mudflats are frequently covered with water and are exposed mainly after cold fronts with associated north and northwest winds (Mitchell & Boyd 1992). Seagrasses (primarily *Halodule beaudettei*, with some *Thalassia testudinum*, *Syringodium filiforme* and *Halophila engelmannii*) covered a limited area exposed offshore during the period of lowest water levels.

Low Seagrass Flat.—This area includes the intertidal area between Port Isabel and Laguna Heights, north of Texas Route 100. Turtle-grass (*Thalassia testudinum*) covered about half of these low mudflats, which were inundated and exposed on a daily basis by tides throughout most of the winter months.
Methods

Each area was censused every two weeks, as accessibility allowed. Usually, all areas were censused during the same day, although occasionally two days were needed. During some rainy periods, not all areas were censused, due to road conditions. Each study area was censused 15-17 times. The distance to the water’s edge was estimated at reference points during each census. Species were identified based on plumage, silhouette, behavior, and calls (Hayman et al. 1986). Because of frequent identification difficulties, only 4% of all dowitchers were identified to the species level. Therefore, Short-billed and Long-billed Dowitchers were treated as "dowitchers" in this paper. At times, mainly on the low mudflat plot, small sandpipers were lumped as Calidris spp. ("peeps") due to distance. This category does not include the Stilt Sandpiper (C. himantopus), a much larger species. 10 X 40 binoculars were used to scan for shorebirds, and a 15-45 X zoom telescope was used to identify most individuals. During each census, microhabitat use was recorded for each species, as shallow water only, shallow water and exposed mud, or exposed mud only.

Results

General patterns.—A total of 23 shorebird species (Table 1) were observed on the study plots, with 19 species recorded in numbers averaging at least one individual per census on at least one study plot (Table 1). The highest number of shorebirds present at a single time on a study area was 20,978 birds on High Mudflat/Pool, on 11 January 1994. That plot averaged the highest total numbers of shorebirds, and contained the largest single species total: 16,930 Western Sandpipers, also on 11 January 1994. Eleven species were recorded on all four plots, but three species were restricted to ≤2 study plots (American Avocet, Marbled Godwit, and Stilt Sandpiper). Peak total numbers of shorebirds occurred at different times on each of the four plots (Fig. 1).

High Mudflat/Pool.—The largest numbers of many shorebird species were recorded here. Several species, including American Avocet (peak 1200 on 23 January 1993) and Stilt Sandpiper (peak 480 on 17 December 1992), were essentially restricted to this habitat. Total monthly shorebird numbers peaked in December 1993 and January 1994 (Figure 1), and Western Sandpipers averaged 48% of the shorebird community. Total shorebird numbers peaked during low water (Fig. 2). Least Sandpipers reached peak abundance here (Table 1) and foraged
Table 1. Mean and maximum (in parenthesis) numbers of shorebirds for species averaging at least 1/census on at least one study plot, Lower Laguna Madre, November-February 1992-1993 and 1993-1994. Asterisk (*) indicates highest mean or maximum for a given species.

<table>
<thead>
<tr>
<th>Avian Species</th>
<th>Habitat Type</th>
<th>High Mudflat</th>
<th>Low Mudflat</th>
<th>Algal Mudflat</th>
<th>Seagrass Flat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-bellied Plover,</td>
<td></td>
<td>77.4 (320)</td>
<td>*246.9 (1450)</td>
<td>1.1 (5)</td>
<td>17.5 (75)</td>
</tr>
<tr>
<td>(Pluvialis squatarola)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snowy Plover (Charadrius alexandrinus)</td>
<td></td>
<td>*17.9 (51)</td>
<td>1.2 (21)</td>
<td>8.0 (36)</td>
<td>0.0 (0)</td>
</tr>
<tr>
<td>Semipalmated Plover (Charadrius semipalmatus)</td>
<td></td>
<td>13.1 (91)</td>
<td>2.5 (23)</td>
<td>*14.2 (95)</td>
<td>0.6 (3)</td>
</tr>
<tr>
<td>Piping Plover (Charadrius melodus)</td>
<td></td>
<td>4.9 (24)</td>
<td>2.1 (13)</td>
<td>*5.1 (69)</td>
<td>0.1 (1)</td>
</tr>
<tr>
<td>Killdeer (Charadrius vociferus)</td>
<td></td>
<td>*5.8 (23)</td>
<td>0.9 (5)</td>
<td>0.8 (4)</td>
<td>0.4 (6)</td>
</tr>
<tr>
<td>American Avocet (Recurvirostra americana)</td>
<td></td>
<td>*412.9 (1200)</td>
<td>0.7 (12)</td>
<td>0.0 (0)</td>
<td>0.0 (0)</td>
</tr>
<tr>
<td>Greater Yellowlegs (Tringa melanoleuca)</td>
<td></td>
<td>*52.4 (198)</td>
<td>16.2 (110)</td>
<td>3.6 (12)</td>
<td>1.7 (10)</td>
</tr>
<tr>
<td>Lesser Yellowlegs (Tringa flavipes)</td>
<td></td>
<td>*69.8 (360)</td>
<td>22.9 (270)</td>
<td>3.2 (15)</td>
<td>0.2 (3)</td>
</tr>
<tr>
<td>Willet (Catoptrophorus semipalmatus)</td>
<td></td>
<td>127.7 (590)</td>
<td>*261.5 (1100)</td>
<td>1.5 (6)</td>
<td>99.7 (400)</td>
</tr>
<tr>
<td>Long-billed Curlew (Numenius americanus)</td>
<td></td>
<td>0.1 (1)</td>
<td>*71.2 (205)</td>
<td>0.0 (0)</td>
<td>4.8 (25)</td>
</tr>
<tr>
<td>Marbled Godwit (Limosa fedoa)</td>
<td></td>
<td>0.0 (0)</td>
<td>*37.7 (55)</td>
<td>0.0 (0)</td>
<td>0.0 (0)</td>
</tr>
<tr>
<td>Ruddy Turnstone ( Arenaria interpres)</td>
<td></td>
<td>0.1 (2)</td>
<td>*3.8 (12)</td>
<td>0.3 (4)</td>
<td>0.9 (6)</td>
</tr>
<tr>
<td>Sanderling (Calidris alba)</td>
<td></td>
<td>*1.3 (7)</td>
<td>1.0 (8)</td>
<td>0.5 (6)</td>
<td>0.0 (0)</td>
</tr>
<tr>
<td>Western Sandpiper (Calidris mauri)</td>
<td></td>
<td>*2259.1 (16930)</td>
<td>390.9 (4370)</td>
<td>36.4 (208)</td>
<td>58.5 (800)</td>
</tr>
<tr>
<td>Least Sandpiper (Calidris minutilla)</td>
<td></td>
<td>*281.7 (1320)</td>
<td>4.1 (40)</td>
<td>61.0 (500)</td>
<td>0.0 (0)</td>
</tr>
<tr>
<td>Peep spp. (Calidris spp.)</td>
<td></td>
<td>330.0 (2000)</td>
<td>*1156.5 (7700)</td>
<td>33.3 (500)</td>
<td>10.0 (150)</td>
</tr>
<tr>
<td>Dunlin (Calidris alpina)</td>
<td></td>
<td>*367.3 (1960)</td>
<td>85.9 (640)</td>
<td>3.5 (30)</td>
<td>11.9 (124)</td>
</tr>
<tr>
<td>Stilt Sandpiper (Calidris himantopus)</td>
<td></td>
<td>*126.0 (480)</td>
<td>0.0 (1)</td>
<td>2.4 (35)</td>
<td>0.0 (0)</td>
</tr>
<tr>
<td>Dowitcher spp. (Limnodromus spp.) 2</td>
<td></td>
<td>556.0 (2000)</td>
<td>*660.4 (2290)</td>
<td>191.6 (1340)</td>
<td>69.7 (600)</td>
</tr>
</tbody>
</table>

Total 3 (Maximum 4)  
*4704.8 (20978) 2966.5 (11980) 366.6 (1932) 276.8 (1528)

1 Other species, detected in lower numbers, include Wilson's Plover (Charadrius wilsonia), American Oystercatcher (Haematopus palliatus), Red Knot (Calidris canutus), and Semipalmented Sandpiper (Calidris pusilla).
2 Of the 4% of all dowitches identified by call, 77% were Long-billed Dowitchers, Limnodromus scolopaceus, while 23% were Short-billed Dowitcher, Limnodromus griseus.
3 Average number of shorebirds, all species combined, per census.
4 Maximum number of shorebirds, all species combined, present during the same census.
Table 2. Winter foraging locations of shorebirds along the Lower Laguna Madre. Species in shallow water and exposed mudflat categories were observed foraging in those habitats on ≥95% of observations. Asterisk (*) indicates species that were exclusively foraging in shallow water or exposed mudflat.

<table>
<thead>
<tr>
<th>Shallow water</th>
<th>Exposed mudflat</th>
<th>Water/mudflat</th>
</tr>
</thead>
<tbody>
<tr>
<td>American Avocet *</td>
<td>Black-bellied Plover</td>
<td>Willet</td>
</tr>
<tr>
<td>Greater Yellowlegs</td>
<td>Snowy Plover *</td>
<td>Long-billed Curlew</td>
</tr>
<tr>
<td>Lesser Yellowlegs</td>
<td>Semipalmated Plover *</td>
<td>Marbled Godwit</td>
</tr>
<tr>
<td>Stilt Sandpiper *</td>
<td>Piping Plover *</td>
<td>Western Sandpiper</td>
</tr>
<tr>
<td></td>
<td>Sanderling</td>
<td>Dunlin</td>
</tr>
<tr>
<td></td>
<td>Killdeer *</td>
<td>Dowitchers</td>
</tr>
<tr>
<td></td>
<td>Ruddy Turnstone *</td>
<td>Least Sandpiper</td>
</tr>
</tbody>
</table>

both on wet and dry mudflats and among Salicornia. Species in the water-foraging group regularly occurred in large numbers here (Table 2). During each winter, such pool-users peaked in December and January, but monthly averages fluctuated relatively little, compared to numbers of the shorebird community as a whole (Figures 1 & 3). Large pool-using species such as American Avocets often foraged in or near ardeids, such as Reddish Egret (Egretta rufescens) and Snowy Egret (Egretta thula), which often occurred in large numbers.

Small plovers, including Piping Plover, Snowy Plover, and Semipalmated Plover, occurred mainly on High Mudflat/Pool and on High Algal Mudflat. They were observed in small, loose flocks away from or at the edge of larger groups of other mudflat foragers. Plover numbers varied considerably, with lowest numbers in January 1993 and February 1994 (Figure 4). Piping Plovers averaged ≥10/census only in November 1992 and December 1993. Snowy Plovers peaked during November-December of each winter, but they remained fairly common until February 1994. In contrast, Semipalmated Plovers were uncommon during most of the first winter but became fairly common during December 1993 and January 1994. Snowy Plovers foraged both near and far from the water’s edge, while Piping and Semipalmated Plovers foraged mainly on the wet flats near the water’s edge (below the glasswort zone, once it became established).

High Algal Mudflat.— This area supported lower numbers of shorebirds, and was used sporadically (Figure 1). Peak numbers occurred during intermediate water levels, with more limited use during peak low or high water (Figure 2). Least Sandpipers were the most common Calidris sandpiper identified here and often foraged near small
Figure 1. Monthly mean number of shorebirds wintering on study areas along the Lower Laguna Madre. See text for description of habitats. Please note that vertical scales differ in all graphs.

plovers. Flocks of dowitchers occurred erratically. Mixed flocks of small plovers consistently occurred here during only November-December 1992. Peak plover numbers were 95 Semipalmated Plovers on 27 November 1992, and 69 Piping Plovers on 14 November 1992. However, small plovers were nearly absent during the second winter and were never seen foraging among the glasswort.

Low Mudflat.—This area, along Bayside Drive, was used heavily by shorebirds during extreme low water conditions in November 1993 and January 1994 (Figures 1 & 2). Peak numbers for the following widespread shorebirds were recorded on this plot: *Calidris spp.*: 7700 on
Figure 2. Relationship of water level and shorebird numbers on study areas along the Lower Laguna Madre. Both axes are scaled logarithmically (base 10). Please note different vertical scales on different graphs.

5 January 1994; dowitchers: 2290 on 5 January 1994; Black-bellied Plover: 1450 birds, on 27 November 1993; and Willet: 1100 on 11 January 1994. Western Sandpipers were common to abundant, while Dunlin were occasionally common. Least Sandpipers were uncommon (max. 40 individuals). Small plover flocks were limited to extreme low water conditions, during which they foraged on moist offshore bars with *Calidris* sandpipers and Black-bellied Plovers.

The largest shorebird species, Long-billed Curlews and Marbled Godwits were essentially or entirely restricted to Low Mudflat. Long-
billed Curlews peaked at 205 on 26 November 1993, while Marbled Godwits peaked at 150 on 17 December 1992. Both these species were often seen in relatively deep water, near Reddish Egrets, Great Egrets (Casmerodius albus) and White Ibis (Eudocimus albus). Curlews foraged in loose flocks of 10-50 or in small groups of 2-3 birds, and were often observed flying between the intertidal flats and inland areas of LANWR. They foraged by probing into the exposed mud and into mud or seagrass below shallow water. Godwits usually occurred in more compact, larger flocks, when present. They foraged on exposed wet mud or in shallow water, and were never observed flying inland.

Low Seagrass Flat.—This long, linear study area was utilized by a limited number of shorebirds, mainly during low water (Figures 1 & 2). Only Willets occurred here in large numbers (peak 400 on 16 December 1993), but dowitchers, Black-bellied Plovers, and Western Sandpipers occurred in modest numbers during low water. Willets foraged frequently in turtle-grass when its tops were exposed, along with some Long-billed Curlews, Reddish Egrets and Tricolored Herons (Egretta tricolor). The other shorebirds foraged on the bare, moist mudflats exposed during lowest water conditions. Peak monthly averages of all shorebirds exceeded 1500 only during January 1994, while shorebirds were absent during the two November 1993 censuses (Figure 1).
Discussion and Conclusions

Many shorebirds of several species wintered commonly on the mudflats of the lower Laguna Madre. Although densities could not be determined in an unbiased fashion, specific patterns of habitat use were primarily based on the foraging requirements of each species. Pool-using birds preferred the large enclosed pool on one study area (High Mudflat/Pool) and were relatively consistent in numbers compared to mudflat foragers. The substantial wintering Stilt Sandpiper population on High Mudflat/Pool during the first winter was unexpected, given its winter status in the United States as irregularly uncommon (Oberholser & Kincaid 1974) or casual (AOU 1983). The large, enclosed pool which the Stilt Sandpipers used is typical Stilt Sandpiper habitat (Hayman et al. 1986) but probably represents a rare habitat in the Lower Laguna Madre.

Mudflat and mudflat/pool foragers, dominated by Western Sandpipers and other *Calidris spp.*, fluctuated in response to changing water levels in all study areas. Highest numbers were recorded when extensive flats in the High Mudflat/Pool and Low Mudflat study areas were newly exposed and still moist. When mudflats dried out due to prolonged exposure, such as in High Algal Mudflat, shorebird use declined. Since ideal conditions are partially dependent on wind shifts due to passage of periodic fronts, such use by shorebirds appears to be very opportunistic.
Relative abundances of particular species in the Low Mudflat area were generally similar to those found by Mitchell & Boyd (1992) in the same area (Bayside Drive). Assuming that most of the *Calidris spp.* sandpipers in Low Mudflat were Western Sandpipers, then only Black-bellied Plovers, both yellowlegs, and Marbled Godwits were disproportionately more common during my censuses than Mitchell & Boyd's (1992) in Low Mudflat habitat. The peak of >1400 Black-bellied Plovers appears high, as it represents more than three times the total number seen along the Laguna Madre of Tamaulipas (Morrison et al. 1993). Marbled Godwits, uncommon during this study, may winter in large flocks in the Laguna Madre of Tamaulipas, a similar hypersaline lagoon in northeastern Mexico (Morrison et al. 1993). The nearness of coastal saline prairie to extensive intertidal feeding areas may explain the higher numbers of Long-billed Curlews on Low Mudflat than in my other areas or in Oso Bay (Withers & Chapman 1993). Snowy Plovers and Dunlin were somewhat less common during my censuses than in Mitchell and Boyd (1992), particularly given the generally higher numbers of shorebirds found in this study. The total absence of Black-necked Stilts during this study is inexplicable, given their winter occurrence in the Corpus Christi area (Withers & Chapman 1993).

The modest peak numbers of small *Charadrius* plovers were expected, but the failure of many small plovers to winter in any plots was somewhat unexpected. Open algal flats normally support Snowy and Piping Plovers and Least Sandpipers in the Laguna Madre, but the spread of glasswort onto both algal flats and high mudflats may have made those habitats unsuitable for small plovers. This would be particularly true for Snowy Plovers and Piping Plovers, which forage on somewhat higher flats - the area covered by *Salicornia*. None of the three small plovers was recorded foraging in *Salicornia*-covered areas, even in very open stands. Relatively large numbers of plovers only occurred when damp or wet flats were available above or below the *Salicornia*-covered areas.

Shorebird use of the lower seagrass meadows and lower, bay-margin mudflats by large numbers of *Calidris* sandpipers, Willets, and Black-bellied Plovers was linked with cold fronts (northers) and seasonal low water in winter (Breuer 1962). Such low mudflats probably supply abundant food resources for shorebirds when they are exposed. These flats remain moist during short-duration exposures during the cool temperatures of winter. In contrast, the frequently exposed higher mudflats often dry out and are apparently unsuitable for most shorebirds.
in the absence of rainfall (Skagen & Knopf 1993). Shorebirds have seldom been observed previously foraging in seagrass, except in intertidal areas (Dann 1987).

There is variability in all wetland/mudflat ecosystems, but the climatic variability, large size, shallow water, and flatness of the lower Laguna Madre ecosystem appear to make it particularly variable. Areas heavily used one day, month, or season may be little used at another time due to slight changes in water level. During times when neither the High Mudflat/Pool area nor the Low Mudflat area would be suitable for large numbers of mudflat-foraging shorebirds, other nearby areas may be suitable. For example, on the 1993 Laguna Atascosa Christmas Bird Count, >20,000 shorebirds (mainly Western Sandpipers and dowitchers) were recorded on the Buena Vista Ranch, located adjacent to LANWR. Mitchell (1992) noted similar shifts in Redheads (*Aythya americana*) in the Lower Laguna Madre, due to changing water levels.

Evidence to date suggests that (1) extensive areas along an elevational gradient are necessary to support large numbers of wintering shorebirds, and (2) that high mudflats free of *Salicornia* are needed to support wintering flocks of small plovers, including the declining Snowy and Piping Plovers.

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LATE QUATERNARY SEDIMENTATION, LOWER NUECES RIVER, SOUTH TEXAS

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Abstract.—Three valley fill and four alluvial terrace units are recognized from Holocene and late Pleistocene sediments in the lower Nueces River valley where this river is entrenched in the late Pleistocene Beaumont Formation. The three valley fill units are included in the Cayamon Creek Alloformation and are designated (from youngest to oldest) Cayamon Creek allomembers 3, 2, and 1. Allomember 3 consists of late Holocene sands. This is unconformably underlain by the muddy sand of allomember 2. Gastropod shells from this unit were radiocarbon dated at 965 ± 95 YBP. The unconformably underlying allomember 1 consists mainly of coarse sands and gravels. A log buried in this unit has been dated at 13,230 ± 110 YBP. Four late Pleistocene terraces occur at elevations of (1) 0-5.7 m (0-19 ft), (2) 8.4-9 m (28-30 ft), (3) 10.8-13.5 m (36-45 ft), and (4) 14.4-16.5 m (48-55 ft) above the present day flood plain. The four terraces (from youngest to oldest) are the Angelita, Fort Lipantitlan, Bluntzer, and Corpus Christi.

River valleys and their alluvial sediments of the lower Gulf Coastal Plain are the products of changing climate and sea level during the Quaternary. The best studied late Pleistocene and Holocene river deposits of the Texas Coastal Plain are associated with the Colorado River (for summary, see Blum & Valastro 1994). The Nueces River drains an area of 43,900 km², a little more than 40% of the 103,000 km² drained by the Colorado River of Texas (US Bureau of Reclamation 1983). The present study encompasses the lower Nueces River valley, from the mouth of the river in Nueces Bay to Wesley Seale Dam, near Mathis, Texas.

The lower Nueces River valley and its terrace and valley fill deposits are a testament to the effects of changing sea level on the lower Texas coast. At the western edge of the city of Corpus Christi, where IH 37 crosses the Nueces River, the valley floor is more than 25 m below the top of the valley wall of the Beaumont Formation and there is at least another 10 m of latest Pleistocene valley fill below that. This approximately 35 m of erosion is quite remarkable in coastal South Texas, where the land surface slopes gently gulfward at a rate of 0.5 m per km (2.5 ft per mile) (Weeks 1945). This valley contains a complex variety of sedimentary fill.
Terraces are geomorphic features that are recognized on the basis of landscape position. Deussen (1924) was the first to map the terraces of the Nueces River. In the vicinity of Calallen (south of Odem), he recognized two terrace levels. Both are present in the region between San Patricio/Bluntzer and Odem. Price (1933) described these two terraces in greater detail. He named the upper unit the Corpus Christi Terrace and designated its type area as occurring approximately 1.6 km southeast of Odem, at an elevation of 15 m (50 ft). He showed only this upper terrace continuing to the east of Odem to Corpus Christi Bay. This terrace is shown (Price 1933: Fig. 17) offset (down to the coast) by the Clarkwood fault. 3.3 km east of Bluntzer, the terrace is shown occurring at an elevation of 21-24 m (70-80 ft), approximately 15-18 m (50-60 ft) above the floodplain. West of Odem, there is a lower terrace, which he named the Angelita Terrace. The type area for the Angelita Terrace is the surface 5 km to the southwest of Odem at an elevation of 4.5-7.5 m (15-25 ft). Near Bluntzer, it is shown at an elevation of 9-10.5 m (30-35 ft), approximately 4.5 m (15 ft) above the floodplain.

Weeks (1945:1707) apparently considered the gravels of the Angelita Terrace near Calallen (probably the Fordyce pit at San Patricio) equivalent to the Uvalde gravels. He (1945: Fig. 4) showed four terraces above the Nueces River west of Dinero (outside of our study area), where the river is entrenched in the Goliad and/or Fleming Formations, but did not discuss them. The highest terrace near Dinero is approximately 30 m above the river bed; the lowest 9 m. Doering (1956: Fig. 6) showed three terraces in the area between Odem and San Patricio at 3-4.5 m (10-15 ft), 12 m (40 ft), and 15 m (50 ft) above stream level. The uppermost terrace of Weeks (1945) near Dinero is shown as a continuation of the Beaumont surface northwest of Mathis; the lower three correspond to the terraces near Odem. Doering (1956) interpreted that the two upper terraces between Odem and Bluntzer were equivalent to the Corpus Christi Terrace as defined by Price (1939). Doering (1956) concluded that the middle terrace correlated with the single Corpus Christi Terrace east of the Clarkwood fault and restricted the name to this unit. He suggested that the upper terrace was equivalent to the Eunice (Sixth Street) Terrace of the Colorado River.

Conkin et al. (1962) studied gastropod and other fossils from the Fordyce Quarry near San Patricio. This quarry is within the Angelita Terrace of this report. They determined that the terraces were late Wisconsinan based on fossil evidence. The Geologic Atlas of Texas
(Barnes 1975) recognized three sets of exposed (Deweyville) terrace deposits at 1.5-6 m (5-20 ft), 6-9 m (20-30 ft), and 12-16.5 m (40-55 ft) above the Recent Nueces floodplain. Baskin (1991) reported reworked early Pliocene horse remains along with late Pleistocene fossils in the Angelita Terrace near Odem and in the valley fill near Bluntzer.

The present study has the advantage of more detailed USGS topographic maps (7.5 minute series, 1" = 2000’) available in 1969 and 1979, as compared to 15 minute series maps (1" = 5280’) prior to those years. This study recognizes four terraces (Figs. 1 & 2) at the following elevations above the floodplain: (1) 0-5.7 m (0-19 ft), (2) 8.4-9 m (28-30 ft), (3) 10.8-13.5 m (36-45 ft), and (4) 14.4-16.5 m (48-55 ft). The lowest terrace corresponds with Price’s Angelita Terrace. The Angelita is distinctive in possessing large meander loops with a mean radius of curvature of 900 m. It dips below the floodplain in the lowest reaches of the floodplain, as illustrated by Price (1933).

The second terrace probably is equivalent to the middle terrace of the Geologic Atlas and is here given the name Fort Lipantitlan Terrace. The Fort Lipantitlan Terrace is named for the type area at the Fort Lipantitlan historical site on the south side of the Nueces River valley, 4.8 km due west of San Patricio at an elevation of 19.5 m (65 ft). The third terrace is equivalent to Doering’s middle terrace, which occurs at a lower elevation than the type of the Corpus Christi Terrace and herein is called the Bluntzer Terrace. The type area is located 300 m north of Bluntzer along state highway 666 at an elevation of 16.8 m (56 ft). The uppermost terrace correlates with Price’s Corpus Christi Terrace west of the Clarkwood fault. This terrace is equivalent to the uppermost of Doering’s (1956) three terraces.

Nueces River Allostratigraphic Units

An additional unit, the Cayamon Creek Alloformation, is recognized for the valley fill beneath the present day floodplain between Odem and Sandia (Figs. 1 & 2). Allostratigraphic units are three-dimensional sedimentary units that are delimited by their bounding unconformities (North American Commission on Stratigraphic Nomenclature 1983). This unit is defined from two sections measured at the Wright Materials, Inc. quarries in Nueces County on the south side of the Nueces River, 4 and 4.5 km respectively south southwest of San Patricio. The surface elevation of the quarries is approximately 10 meters above sea level, the level of the flood plain. A pump is used to lower the water level and the pits are quarried by a drag line. The drag-lines quarry a total of 13
Figure 1. Cross sections of the Nueces River valley. A. cross section from south of Fort Lipantitlan to near Willow Lake. B. cross section from Bluntzer through the gravel pits to San Patricio. Locations of sections are shown in Figure 2. Abbreviations: AT, Angelita Terrace; BF, Beaumont Formation; B/LF, Beaumont and/or Lissie Formation; BT, Bluntzer Terrace; c, colluvium; CAla, Cayamon Creek Allomember 1, sandy gravel unit; CCA, Cayamon Creek Alloformation; CA1b, Cayamon Creek allomember 1, sand and muddy sand units; CA2, Cayamon Creek allomember 2; CA3, Cayamon Creek allomember 3; CCT, Corpus Christi Terrace; LF, Lissie Formation; LT, Fort Lipantitlan Terrace; NP, north pit, Wright Materials, Inc.; NR, Nueces River; and SP, south pit, Wright Materials, Inc.

to 15 meters from the surface. The lower one to two meters are under water even during pumping. Quarrying is halted on encountering a yellow-green clay, presumably representing the Beaumont Formation, or a calcareous-cemented sandstone. This sandstone could possibly represent the Goliad Fm., but it is also encountered at the Odem locality (Baskin 1991) which is too far downdip to encounter the Goliad at such a shallow depth. A 14 meter section (Baskin & Cornish 1989) was measured in the north wall of a pit 1 km northeast of FM 3088 (Figs. 1 & 2: NP). A 13.5 meter section was measured in the northwest wall of a pit 0.7 km southwest of FM 3088 (Figs. 1 & 2: SP).

The Cayamon Creek Alloformation can be subdivided into three allomembers: allomember 1, the lowermost sand and gravel dominated unit; allomember 2, a mud dominated unit; and allomember 3, a fine sand unit. Allomember 1 is by far the thickest of the three.

The lower 3 to 4 meters of allomember 1 are dominated by gravel. The coarsest material is from the base of the section (mainly underwater). The long diameter of the 20 largest cobbles easily visible at the base of the gravel pit section had an average diameter of 13.5 cm and a maximum diameter of 18 cm. The lower 1.5 to 2.5 m are mainly a sandy pebble gravel, with crudely horizontal and tabular-planar bedding (up to 60 cm thick), interbedded with cross-bedded sand.
Figure 2. Map of the Nueces River valley showing stratigraphic units in the area of study. Contours are taken from the San Patricio quadrangle, USGS 7.5 minute series. The lines passing through A" and through B-B' show the locations of the cross sections shown in Figure 1. Abbreviations are those of Figure 1.

Pebble imbrication is present, but rare. The sandy gravel consists of 55-65% gravel, 35-45% sand, and 1-2% mud, and has a bimodal distribution, with modes at approximately 5.75 and 0.30 mm. The cross-bedded sand has a modal value of 0.21 mm and contains about 90% of sand and 5% of mud and gravel respectively. The bottom part of the unit includes two or three major cut and fill events. Gravel units are separated by 20 to 50 cm beds of slightly gravelly muddy sands.
The next 1.5 m are mainly sand, arranged in lateral accretion units dipping 4-5°. The predominant sedimentary structure in this subunit of the section is tabular-planar cross-bedding (up to 1 m thick), as well as trough cross-bedding. Within and at the top of the unit there are thin gravel lenses. The sands are moderately well to very well sorted and have mean size ranges of 0.25 to 0.18 mm. The top of this unit is marked by a locally thin sandy gravel capped by a sandy mud.

The next 4 m consist of alternating muddy sands and sandy muds. The beds are 5 to 30 cm thick, with a tendency for thinner beds higher in the section. A possible soil horizon occurs about 1 m above the base of this unit. Near the top of the unit are scattered, small caliche nodules.

Allomember 2 unconformably overlies the lower unit and varies in thickness from 2 to 3 m. It is a sandy mud that ranges from a light orange below to dark-gray or black at the top. The dark sandy clay has a rich terrestrial and fresh-water gastropod fauna. The upper unit (allomember 3) is a poorly-exposed, fine sand that is channeled into the underlying units. This unit is not present at the south pit.

Fluvial Architecture of the Cayamon Creek Alloformation

Cayamon Creek allomember 1 has an overall fining-upward trend, related to decreasing flow strength and depth, but the lower part of the section, in particular, records several cut and fill episodes. Thickness of individual units can vary considerably over distances of tens of meters, presumably related to variation in distance from the axis of the paleochannel. The basal gravel, cut and fill, vertical decrease in grain size, lateral accretion bedding, and the suite of sedimentary structures described above all indicate that allomember 1 was deposited by a coarse-grained meandering fluvial system. Coarse-grained meandering fluvial systems are well described by Bluck (1971), McGowan & Garner (1970), and Jackson (1978), among others.

The coarsest material from the base of the section represents channel lag deposits. The gravel cobbles consist mainly of brown chert derived from Cretaceous carbonates of the Edwards Plateau, black chert from the Maravillas Formation of West Texas, caliche from the nearby Goliad Formation, and silicified wood from Tertiary Coastal Plain sediments (Russell 1981). There are also clay galls, derived from the underlying Beaumont Formation. Long, intermediate, and short diameters were measured for a sample of the 13 largest chert cobbles easily visible at
the base of the section. The mean intermediate diameter is 7.8 cm. Five large cobbles from the sorted material pile had a mean intermediate diameter of 10.3 cm. Gustavson (1978) recorded mean intermediate clast length for the 10 largest cobbles from 13 sample sites along the upper Nueces River south of the Balcones Escarpment as ranging from 3.5 to 10.8 cm. Velocities of about 3-6 m/sec at 1-10 m above the stream bed are required to transport particles this size (Sundborb 1956). Floods this size occur at an average interval of 8 years on the upper Nueces (Gustavson 1978). Similar velocities must have been in force in the lower Nueces in the late Pleistocene. Runoff from major tropical storms and hurricanes is probably sufficient to account for this stream competence. The maximum discharge for the Nueces River at Three Rivers (72 km upstream from the study area) since 1875 was 3,950 m$^3$/sec following Hurricane Beulah on 23 September 1967. The previous maximum flow was 2,380 m$^3$/sec on 18 September 1919 after a major hurricane. The maximum recorded flow for the Nueces River at Mathis before the construction of the Wesley Seale Dam was 1,650 m$^3$/sec on 20 September 1919.

The sand-dominated, lateral accretion beds represent point bar deposits. Gravel lenses in this unit could represent some minor abandoned channel fill units or chute bars.

The uppermost alternating sequence of sands and muds result from overbank crevasse splay deposition or near-channel levee deposits. These are similar to "rhythmites" in crevasse splay sequences of the Mississippi River (Farrell 1987) that developed by overbank sheet floods and were deposited by waning flow. They represent vertical accretion of the flood plain. Subaerial exposure is indicated by numerous caliche zones, similar to flood plain deposits on the Brazos River (Bernard & Major 1963).

Allomembers 2 and 3 represent early to late Holocene floodplain deposits. They may be contemporaneous modern deposits of the Nueces River and represent flood plain muds and channel/point bar sands, respectively, of a muddy meandering fluvial system.

Chronostratigraphy

Formation of the Nueces River terraces and valley fill is related to changing climate and sea level during the late Quaternary. Possible age relationships of the alluvium to oxygen isotope stages are discussed in Baskin (1991). The Angelita Terrace predates the late Wisconsinan
maximum drop of sea level and is probably equivalent in age to the Eagle Lake Alloformation of the lower Colorado River (Blum & Valastro 1994), where the river is cut into the alluvial plain of the Beaumont Formation. Blum & Valastro (1994) correlated the Eagle Lake Alloformation with the Sixth Street Terrace in the Austin area and stated that deposition of this unit took place from 20,000 to 14,000 YBP. The Nueces River valley was excavated at least 35 m into the Beaumont Formation during the maximum drop in sea level during isotopic stage 2, approximately 15,000 YBP (Baskin 1991). Blum et al. (1994) stated that excavation of bedrock valleys in the Edwards Plateau by the Colorado River took place from about 14,000 to 11,000 YBP.

Following the late Wisconsinan low stand, sea level began to rise (oxygen isotope stage 1), continuing on into the Holocene, reaching its present level about 5000 YBP. Broecker et al. (1988) stated that large meltwater influxes into the Gulf of Mexico began around 14,000 YBP, peaked rapidly around 12,500 YBP, and then decreased rapidly. This time of rapid melting and concomitant sea level rise corresponds to the time of onset of deposition of the valley fill deposits. Toomey et al. (1993) stated that cave faunas from the Edwards Plateau indicate that average summer temperatures increased rapidly from 15,000-13,000 YBP to near present values and that effective moisture decreased and then increased again from 14,000-10,500 YBP. This time of dry conditions on the Edwards Plateau corresponds to meltwater discharge peaks in the Gulf of Mexico. Blum et al. (1994) stated that deposition of complex valley fills took place in the last 11,000 years. Cayamon Creek allomember 1 of the Nueces River valley corresponds with Columbus Bend Allomember 1 of the lower Colorado River, which was deposited from approximately 12,000 to 5,000 YBP (Blum & Valastro 1994). The oldest date they reported for this unit is 12,970 ± 640 YBP. However Lundelius (1992) reported a radiocarbon date of approximately 15,000 YBP for the equivalent First Street Terrace in Austin. This and the radiocarbon date for the Cayamon Creek allomember 1 may indicate that deposition of the valley fill may have begun somewhat earlier than 12,000 YBP.

Pleistocene fossils and a piece of wood that was radiocarbon dated were collected in place in the cross-bedded gravelly sands and sandy gravels of Cayamon Creek allomember 1. The wood was from the north pit, approximately 4 m above the base of the section. The sample was dated by the Southern Methodist University Radiocarbon laboratory following a partial cellulose extraction pretreatment. The fractionation
corrected $^{14}$C age for sample SMU 2306 is $13,230 \pm 110$ YBP with a $\delta^{13}$C of -26.3\% (Haas, pers. comm.). The wood sample had absorbed large amounts of sulfur, which may indicate deposition in a swampy environment (Haas pers. comm.) In the gravels in the lower part of the section are scattered lenses of pebbles coated with manganese dioxide.

Cayamon Creek allomember 2 corresponds to Blum et al.'s (1994) Columbus Bend Allomember 2, which was deposited from approximately 5,000 to 1,000 YBP. The snail-bearing upper unit of allomember 2 has a C-13 corrected date on snail shells of $965 \pm 95$ YBP with a $\delta^{13}$C of -8.5\% (Krueger Enterprises, Geochron Laboratories sample GX-19928). This unit may be the same as Conkin et al.'s (1962) snail bearing unit from the top of the Fordyce Quarry, which they concluded was late Pleistocene. Toomey et al. (1993) suggested that the Edwards Plateau was experiencing relatively more mesic conditions from 2500-1000 YBP. This may explain the cooler and more humid conditions indicated by the Fordyce snails that Conkin et al. (1962) thought were indicative of a late Wisconsinan age.

**Conclusions**

The formation of Gulf Coast terraces was first addressed in detail by Fisk (1944). He related Mississippi Valley terrace levels to glacio-eustatic sea level changes: sea level highstands caused floodplain formation, while lowstands caused downcutting through the flood plains, leaving behind an elevated terrace. It is implicit in this theory that all rivers debouching into the Gulf of Mexico should have similar terrace sequences. However, several recent studies suggest that climate as well as glacio-eustatic changes affect terrace formation. Blum & Valastro (1994) suggested that changes in climate, coupled with degradation of upland soil mantles, affected the rate of runoff and sedimentation rates.

Chronostratigraphic correlation of valley fill/terrace sequences between the Nueces River and the Colorado River support an argument against strict glacio-eustatic controls for terrace formation. In the Colorado River valley, the Columbus Bend Allomember 2 and Eagle Lake Allomember are exposed as terraces in the upper reaches of the valley (Blum and Valastro, 1994). However, these terraces are buried below the modern flood plain in its lower reaches. This effect is apparent for the Angelita Terrace of the Nueces River valley. Within the study area, it dips from 9 m above the valley floor, just below the Wesley Seele Dam to floodplain level immediately east of IH 37.
The chronostratigraphic equivalent of the Columbus Bend Allomember 2 is the Cayamon Creek allomember 2, which is not exposed as a terrace, but as floodplain valley fill. This downdip change in relative terrace height indicates that terrace height above the valley floor is not useful for between-valley correlations. Four terraces in the Nueces valley would not necessarily correlate to four terraces in any other valley. Different dates for similar late Pleistocene terrace levels in different valleys caused controversy among workers using the Fisk concept. Some researchers found it easy to dismiss other workers' radiocarbon dates that did not fit their model. Now, with more chronostratigraphic studies and a different concept of terrace formation, researchers should be able to piece together the complex history of external controls on late Quaternary Gulf Coast fluvial processes.

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ENVIRONMENTAL ASSESSMENT OF LA QUINTA CHANNEL, CORPUS CHRISTI BAY, TEXAS

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Abstract.—Benthic invertebrate communities sampled during 1992 and 1993 from each of three stations in La Quinta Channel and Corpus Christi Bay were analyzed. Higher numbers of individuals were found in the top 3 cm at all stations during each sampling period. Biomass, however, was greater in the bottom (3-10 cm) sediment section. There were higher numbers of species, greater species richness, and more evenness in La Quinta Channel than in Corpus Christi Bay. Both communities were dominated by deeper-dwelling equilibrium species and the low abundance of pioneering species. The results of this study indicate that the sediments of La Quinta Channel differ little from those of Corpus Christi Bay. Results are consistent with findings that contamination concentrations are low in the La Quinta Channel when compared to those of Corpus Christi Bay.

Man has caused negative impacts on estuaries in a variety of ways, including chemical pollution, reduced inflow, channelization and suspended wastes. Corpus Christi Bay is a large bay near Corpus Christi, Texas, the sixth largest port city in the United States. Corpus Christi has a population of over 250,000 people. Its metropolitan center is located along the west side of the bay. La Quinta Channel traverses the north shore of Corpus Christi Bay and is a spur of the main Corpus Christi Ship Channel which serves the Port of Corpus Christi (Fig. 1). La Quinta Channel serves several industrial plants, including DuPont Chemical, Reynolds Aluminum, and Occidental Chemical Company. This concentration of industry has led to public concerns about the health of this environment. It is necessary to determine whether or not anthropogenic environmental stresses have affected La Quinta Channel.

Benthic organisms have been especially useful to detect pollution and to estimate overall effects of pollution on a community (Oglesby 1967; Houston et al. 1983; Ferraro et al. 1991). Benthic species and communities, rather than fish or planktonic fauna, have often been regarded as being the best indicators of organic pollution because of their limited mobility (Wass 1967; Flint et al. 1980). For example, an estuary under severe environmental stress will be depauperate of benthic species, while a similar estuary that is relatively unaffected by human activities will generally have a much higher number of benthic species (Marques et al. 1992).
There are several reasons why benthic organisms are good indicators of environmental stress (Soule 1988). (1) Because of gravity, pollutants end up in bottom sediments. Even pollutants in freshwater will be transported to coastal sea bottoms. (2) Living organisms die and end up in the detrital food chain, which is utilized by the benthos. Pollutants are usually tightly coupled to organic matrices, therefore benthos have great exposure through their niche (food) and habitat (living spaces) to pollutants. (3) Benthos are relatively long-lived and sessile and thus integrate the effect of pollutants over long temporal and spatial scales. (4) Benthic invertebrates are sensitive to pollutants. (5) Bioturbation and irrigation of sediments by benthos affect the mobilization and burial of xenobiotic materials.

The objective of this study was to measure the environmental conditions of La Quinta Channel to assess if the Channel has been affected by anthropogenic input. The approach used was to compare the benthic community of La Quinta Channel shoal areas with reference stations in Corpus Christi Bay. This was accomplished by measuring benthic abundance, biomass, and community diversity for one year. The relative
characteristics of the benthos in the two study areas is assumed to be indicative of the environmental conditions present.

**Methods**

**Study Area Description.**—The Corpus Christi Bay system is one of seven major estuarine systems along the Texas Gulf Coast. The open bay bottom surface area totals 432.98 km² (Flint et al. 1983). It is separated from the Gulf of Mexico by a barrier island, Mustang Island. There is one main tidal inlet, Aransas Pass, and two forms of fluvial flow, the main being Nueces River and the other Oso Creek. The ecosystem includes the following bodies of water: Nueces Bay, Corpus Christi Bay, Oso Bay, the northern portion of the upper Laguna Madre, and the southern portion of Redfish Bay (Fig. 1).

Flint et al. (1981) noted that, due to the small volume of riverine input, salinities reflect a more oceanic condition. They also stated that the Corpus Christi Bay system is relatively sensitive to changes from factors such as infrequent surges of freshwater usually occurring from large storms in the watershed.

Bottom sediments within Corpus Christi Bay are primarily mud in the interior portions, with muddy and shelly sands around the shoals (Flint et al. 1980). The composition of the suspended sediment load is primarily inorganic silt and clay detritus, with a subordinate organic skeletal fraction dominated by diatoms (Shideler 1980).

**Sampling Sites.**—A total of six sampling stations (Fig. 1) were examined; three stations in the shoal areas of La Quinta Channel and three reference stations in Corpus Christi Bay away from any obvious anthropogenic influence. The stations were named for their location and station (i.e., Nueces-Corpus Christi/Station C was NCC and La Quinta Channel shoal area/Station A was LQA). Stations NCC (3.4 m) and NCD (2.7 m) are part of a series of stations that have been sampled previously (Montagna & Kalke 1992), and NCE (3.4 m) was added in April, 1991. Samples were collected in October, 1992, and January, April, and July, 1993. The stations in La Quinta Channel are LQA (2.5 m), LQB (1.8 m), and LQC (2.5 m) (Fig. 1). Station LQA was behind Occidental Chemical Company on the south side of the channel, station LQB was in Ingleside Cove, and station LQC was 225 m west southwest of Naval Station Ingleside. The sampling area at each station was 2 m².

**Hydrography.**—Hydrographic measurements were taken just below
the water surface and at the bottom of the water column using a Hydrolab Surveyor II. Data (units and accuracy) were collected on: depth (±1 m), water temperature (±0.15°C), pH (±1 unit), dissolved oxygen (±0.2 mg l⁻¹), specific conductivity (±0.015-1.5 mmhos cm⁻¹ depending on range), redox potential (±0.05 mV), and salinity (±0.7 ppt). Measurements were taken at all stations during each collection.

Sediment.—Sediment samples were taken during the first collection period. Each sample was placed in a jar and filled with distilled water and hydrogen peroxide. The samples were allowed to sit for one week to digest organic material. The samples were filtered, dried, and weighed (mg) (Folk 1964). The percent of rubble, sand, silt, and clay was then calculated.

Benthic Abundance and Biomass.—Benthic abundance and community structure were measured using the standard techniques Montagna & Kalke (1992) have been using since 1984. Samples were collected using core tubes that were 6.7 cm in diameter yielding a sample area of 35.4 cm². The cores were sectioned to sediment depths of 0-3 cm and 3-10 cm to examine the vertical distribution of macrofauna. Each sediment section was stored in 4% Formalin made with filtered sea-water. Animals were extracted with a 0.5 mm mesh sieve. After the species had been identified and enumerated, biomass was measured. Mollusk shells were removed by an acidic vaporization technique (Hedges & Stern 1984). Animals were separated into their major groups: annelids, crustaceans, mollusks, nemerteans, ophiuroids, sipunculids, and others and put on aluminum pans. The pans were dried at 50°C for a minimum of 48 h to obtain dry weight biomass.

Diversity Analyses.—Diversity was calculated using Hill’s diversity number one (N1) (Hill 1973). It is a measure of the effective number of species in a sample, and indicates the number of abundant species. It is calculated as the exponentiated form of the Shannon & Weaver (1949) diversity index \( H' \).

Richness is an index of the number of species present. The obvious richness index is simply the total number of all species found in a sample regardless of their abundances. Hill (1973) named this index \( N_0 \). Another well known index of species richness is the Margalef (1958) index \( R_1 \). \( R_1 \) is based on the relationship between the number of species and the total number of individuals observed.

Evenness is an index that expresses that all species in a sample are
equally abundant. Evenness is a component of diversity. \( E_1 \) is probably the more common, it is the familiar \( J' \) of Pielou (1975). It expresses \( H' \) relative to the maximum value of \( H' \). \( E_1 \) is sensitive to species richness. The variable \( E_1 \) was chosen because it is calculated with \( N_0 \) and \( N_1 \). When \( E_1 \) is equal to 1.0 then there is complete evenness.

Statistical Analyses.—Statistical analyses were performed on sediment, biomass, abundance, and diversity data using general linear model procedures to reveal differences among sampling periods, stations, and sediment depths (SAS 1985). Three-way analysis of variance (ANOVA) models were used where sampling dates, stations, and sediment sections were the three main effects. Two-way ANOVA models were used where sampling dates and stations were the two main effects on total cores. The residuals were tested for conformance to normality using the Shapiro-Wilk statistic (SAS 1985). Orthogonal linear contrasts were used to test the \textit{a priori} null hypothesis that La Quinta Channel stations were different from Corpus Christi Bay stations.

Results

Hydrography.—Mean salinity readings ranged from 23.5 - 30.5 ppt in La Quinta Channel from October 1992 to July 1993, due to rainfall that occurred during the year, especially in May 1993. The trend was similar in Corpus Christi Bay, although the salinity was slightly lower. There was a large seasonal drop in temperature, from 24 C to 13 C, between October and January, but the temperature increased to 40 C by July. The \( pH \) remained constant (7.9 units) and was similar among each of the six stations all year. Dissolved oxygen (DO) concentration in the water had a mean of 7.0 mg \( l^{-1} \) for all stations except NCC and NCD, which were lower (5.5-6.5 mg \( l^{-1} \)), during October. In January and April DO was higher (8.5-9.5 mg \( l^{-1} \)) for all stations. By July it had decreased to 5.0-6.5 mg \( l^{-1} \) and was similar at all stations except for the bottom at NCD, where it was only 1.7 mg \( l^{-1} \). The redox potential remained constant (0.23 mV) during the entire year at all stations. Overall, parameters recorded at each of the stations were very similar to one another.

Sediment.—Sand was predominant at most stations, except for NCC (Fig. 2). The sand content was usually greater in the top 3 cm of the samples. This measurement was taken only once in October, 1992 (NCD was taken October, 1991). All of the La Quinta Channel stations
had sand comprising greater than 75% of the sediment. Both layers at NCC consisted mostly of silt and clay, making up 79.7% in the upper section and 89.2% in the lower section, while there was more sand in NCD (82.4%) and NCE (56.7%).

**Benthic Abundance and Biomass.**—There were more individuals in the top 3 cm of sediment during each study period, except for July 1993 (Fig. 3). The average number of individuals found in the top section for all stations and periods was 13,024 m$^{-2}$, which is 61% of the total average of both sections. The average of the top section at LQA was 12,126 individuals m$^{-2}$, which is lower than in the bottom section (13,307 individuals m$^{-2}$). In October 1992, and January and April 1993, the average density in the upper layer was 67%, while the density was only 41% in the upper layer for July 1993. There were significant interactions (3-way ANOVA, $P=0.0003$) between the sections, dates, and stations for the density.

Average macrofauna density, to 10 cm depth, in La Quinta Channel was not significantly different from Corpus Christi Bay (linear contrast, $P=0.0873$). La Quinta Channel had an average of 25,796 individuals m$^{-2}$ to 10 cm, while Corpus Christi Bay exhibited 20,123 individuals m$^{-2}$.
to 10 cm. The three stations in La Quinta Channel and NCE in Corpus Christi Bay had similar numbers of species throughout the study periods, while NCD was consistently lower (Fig. 3).

La Quinta Channel and Corpus Christi Bay both had a greater biomass (g m$^{-2}$) in the bottom (3-10 cm) sediment section (Fig. 4). La Quinta Channel had an average of 72% and Corpus Christi Bay averaged 69% of the biomass in the bottom sections. Overall, the percent of biomass found in the top 3 cm was 29%, but composition was different among stations. LQA had 17% in the top section, LQB had 35%, there was 39% at LQC, NCC had 23%, NCD was found to contain 50%, and NCE had 33% (Table 1). The high percentage of biomass at NCD occurred in January and April 1993, when NCD had 64% of the biomass in the top 3 cm while the other 2 sampling periods had less than 40% each in the top 3 cm at NCD (Fig. 4). There were significant interactions between the sections, dates, and stations for the biomass (3-way ANOVA, $P=0.0126$).

Biomass in La Quinta Channel to a depth of 10 cm was significantly different from Corpus Christi Bay (linear contrast, $P=0.0112$). La
Quinta Channel had an average biomass of 13.8 g m$^{-2}$ and Corpus Christi Bay had an average biomass of only 10.0 g m$^{-2}$. Without station NCD, the Corpus Christi Bay average biomass would increase to 13.8 g m$^{-2}$.

Polychaetes were the dominant organisms at all stations in both the top and bottom sections of all samples throughout the study period (Table 1). Polychaetes made up 77% of the mean total abundance found in the top 3 cm and 90% for the bottom 7 cm of La Quinta Channel and 84% of the total species in the upper section and 90% in the bottom section of Corpus Christi Bay samples (Table 1). Polychaetes had the greatest biomass at all stations and sections ranging from 0.8 - 9.3 g m$^{-2}$ (Table 1). The biomass of all taxa, except polychaetes, was greater in the top 3 cm than in the bottom 7 cm (Table 1). Polychaete biomass in the bottom section made the overall average biomass of the bottom section greater than that of the top section.

*Benthic Diversity.*—The mean NO (total number of species in a sample) for all stations combined was 18 species. There was a difference in the mean total species between La Quinta Channel (13
Table 1. Vertical distribution of macrofaunal taxa for entire study year, Oct 1992 - July 1993. Mean biomass (g m\(^{-2}\)) and abundance (n m\(^{-2}\)) of taxonomic categories. SD = Standard Deviation.

<table>
<thead>
<tr>
<th>Station</th>
<th>Taxa</th>
<th>0-3 cm</th>
<th>3-10 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>n m(^{2})</td>
<td>g m(^{2})</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>---------</td>
<td>--------</td>
<td>-------</td>
<td>--------</td>
</tr>
<tr>
<td>LQA</td>
<td>Nemertea</td>
<td>449</td>
<td>372</td>
</tr>
<tr>
<td></td>
<td>Polychaeta</td>
<td>544</td>
<td>573</td>
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<tr>
<td></td>
<td>Mollusca</td>
<td>284</td>
<td>270</td>
</tr>
<tr>
<td></td>
<td>Other</td>
<td>142</td>
<td>226</td>
</tr>
<tr>
<td></td>
<td>Ophiuroidea</td>
<td>95</td>
<td>140</td>
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<td></td>
<td>Polychaeta</td>
<td>10,613</td>
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<td>TOTAL</td>
<td>12,127</td>
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<tr>
<td>LQB</td>
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<td>473</td>
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<td>Mollusca</td>
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<td>Polychaeta</td>
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</tr>
<tr>
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<td>Mollusca</td>
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<td>534</td>
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<td></td>
<td>Ophiuroidea</td>
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<td>237</td>
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<td></td>
<td>Polychaeta</td>
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<td>TOTAL</td>
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<tr>
<td>NCE</td>
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<td>Polychaeta</td>
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<td>470</td>
</tr>
<tr>
<td></td>
<td>Other</td>
<td>307</td>
<td>307</td>
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<td></td>
<td>Ophiuroidea</td>
<td>165</td>
<td>225</td>
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<tr>
<td></td>
<td>Polychaeta</td>
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<td>3,237</td>
</tr>
<tr>
<td></td>
<td>TOTAL</td>
<td>11,061</td>
<td>7,535</td>
</tr>
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</table>
species) and Corpus Christi Bay (9 species) (linear contrast, $P=0.0001$) (Fig. 5). There were no significant interactions between dates, stations, and sections for NO (3-way ANOVA, $P=0.1919$). The highest number of species was found in LQC.

The mean number of dominant species (N1) was slightly lower (11 species) than NO, because it takes into account only the number of abundant species. La Quinta Channel (12 species) was different from Corpus Christi Bay (9 species) (linear contrast, $P=0.0001$). There were significant interactions between dates, stations, and sections for N1 (3-way ANOVA, $P=0.0018$).

There was a significant difference between the stations in La Quinta Channel and in Corpus Christi Bay for R1, species richness (linear contrast, $P=0.0001$). The La Quinta Channel stations had a mean of 4.6 compared to 3.5 found among Corpus Christi stations. The overall mean for R1 is 4.0. There was a significant interaction between dates, stations, and sections (3-way ANOVA, $P=0.0277$).

There was a high degree of evenness. The mean E1 for all stations throughout the year was 0.8. There was a significant difference
Figure 6. Species dominance curves for macrofaunal density in the La Quinta Channel and Corpus Christi Bay. Percent abundance vs. species rank for all samples combined.

(P=0.0001) between La Quinta Channel (0.82) and Corpus Christi Bay (0.72). Station NCD had the two lowest evenness indices and it was the lowest in evenness 75% of the time (Fig. 5). During April, however, it had the highest degree of evenness, which was the second highest evenness value overall. There was a significant interaction between dates, stations, and sections (3-way ANOVA, P=0.0001).

Station NCD had the least evenness and had a dominance-diversity curve different from all other stations (Fig. 6). The curves of the other stations were not significantly different from each other and exhibited good evenness. Station NCC had a curve similar to NCD, though not as steep.

Polychaetes were the dominant taxa at all stations during the entire study period. The dominant species throughout the entire study was Mediomastus ambiseta, with a combined average of 25,906 individuals.
m² from all stations for the entire year. This subsurface deposit-feeding species was most abundant at NCC (6,264 individuals m²).

Discussion and Conclusions

The objective of this study was to determine if La Quinta Channel, an area that supports industrial activity, has suffered any environmental degradation relative to other areas of Corpus Christi Bay that do not have such influences. The approach was to take sediment samples and analyze the benthic community. Benthos can be affected by natural influences as well. One must examine natural environmental factors that explain or influence the benthos to assess the relative role of anthropogenic disturbances. For this purpose, we measured sediment grain size was measured during the first sampling period and hydrography was measured at the top and bottom of the water column at each station during each sampling period.

Sediment was most similar between stations LQA, LQB, LQC, and NCD, which are all stations in bay margin areas. Shideler (1980) and Flint & Younk (1983) noted that the shoals of Corpus Christi Bay were made up of muddy and shelly sand. Sand made up greater than 75% of the total sediment composition at these stations. The sand was fine and muddy enough to allow Mediomastus ambiseta to inhabit these areas. Previous studies performed near the location of LQC show that the sediment is made up primarily of fine sand with small amounts of shell (Flint et al. 1980; Flint & Kalke 1986). The stations that were located more towards the middle of the bay, NCC and NCE, were mainly muddy, which is also noted in the study done by Shideler (1980). In a previous study (Montagna & Kalke 1992) NCC had an average of 7.9% sand and NCD had an average of 74.5% sand, which was comparable to the 10.5% and 82.4% found in this study. In general, the sediment characteristics were similar at all stations, except NCC, indicating that differences among stations were probably not due to differences in sediment texture. Mannino & Montagna (1995) found that freshwater inflow was more important in regulating community structure and composition than sediment grain structure in adjacent Nueces Bay.

Odum (1969) proposed a conceptual model for succession based on terrestrial observations. This model suggests that in the early stages of succession (the time following a recent disturbance) a pioneering species is the first to inhabit the area. These organisms are r-selected (i.e. they have short life cycles and high rates of reproduction). With time, the disturbed area matures and the organisms that move in are k-selected
(i.e. they have longer life cycles and lower rates of reproduction). Rhoads et al. (1978) applied this theory of ecological succession to marine benthos to suggest ways that dredge-spoil could be managed to enhance productivity. They reasoned that the organisms in the mature stage are larger than those in the early stage and they are found deeper in the sediment. This means that, in the mature stage, the surface sediments would have a greater abundance of organisms, but the subsurface sediments would have a higher biomass. In the benthos, the pioneering species are suspension feeders or surface deposit-feeders (Kennish 1986). The mature stage species are subsurface deposit-feeders in the benthos (Kennish 1986). The additional number of species present in the mature stage suggests species diversity is higher in relatively undisturbed sediments. Since the study by Rhoads et al. (1978), numerous other studies have demonstrated benthic biological diversity to be an excellent indicator of environmental health (Flint et al. 1980; Flint & Younk 1983; Kennish 1986; Gray et al. 1988).

In the current study, abundance was greater in the top (0-3 cm) sediment section and the biomass was greater in the bottom sediment section (3-10 cm) of sediment. On average, there were 2500 more organisms m⁻² in the surface sediment than in the subsurface sediment in La Quinta Channel compared to 7330 organisms m⁻² in Corpus Christi Bay stations (Table 1). On average, there were 6.18 g m⁻² more in the bottom section than top section in La Quinta Channel and 3.86 g m⁻² in the Corpus Christi Bay stations (Table 1). So, there were differences in the vertical distribution of organisms in La Quinta Channel and Corpus Christi Bay. The difference was more surface dwellers and lower subsurface biomass in Corpus Christi Bay relative to La Quinta Channel. Using the logic in the succession model, this finding indicates that there is no evidence that La Quinta Channel is more disturbed than Corpus Christi Bay. In fact, the reference stations could be more disturbed than the La Quinta Channel stations. The vertical diversity differences (3 more species in surface sections) were identical in both locations.

*Mediomastus ambiseta* was the most abundant and ubiquitous species throughout the current study. *Mediomastus ambiseta* is a non-selective subsurface-deposit feeding polychaete (Fauchald & Jumars 1979; Flint et al. 1980; Flint & Kalke 1986). It is considered an equilibrium species. It is a *k*-selected species that oxygenates the deeper sediment strata by building tubes; *M. ambiseta* is then able to inhabit the deeper sediments (Flint et al. 1980). It was the most dominant species at each station during each sampling period, with the exceptions of NCC and
NCD in October 1992 and NCD in April 1993. This polychaete was compared to the one identified earlier as *M. californiensis* in previous studies (Holland et al. 1973; Holland et al. 1974; Holland et al. 1975; Flint et al. 1980; Flint et al. 1981; Flint & Younk 1983; Flint et al. 1983; Flint & Kalke 1986; Montagna 1989; Montagna & Kalke 1992) and was determined to be the same species, but had been misidentified until a couple of years ago (Kalke, pers. comm.). The overall dominance of *M. ambiseta* at all stations, except NCD, is consistent with the hypothesis that there is no more disturbance in La Quinta Channel than in Corpus Christi Bay.

Pioneering species are those benthic organisms that are *r*-selected and are the first group to colonize an area of recent disturbance, either natural or anthropogenic in nature. Pioneering species were found in small numbers at all stations during this study. Pioneering species that occurred in this study and previous studies (Flint et al. 1980; Flint & Younk 1983; Flint & Kalke 1986; Montagna & Kalke 1992) include: *Streblospio benedicti*, *Parapriniospion pinnata*, *Apropriospion pygmeae*, *Minuspio cirrifera*, *Onuphis eremita oculata*, *Owenia fusiformis*, *Mulinia lateralis*, and *Abra aequalis*. High numbers of pioneering species were found at stations NCC and NCD in October 1992 and with station NCD in April 1993. This may be an example of an early succession community, possibly indicating a type of disturbance. In October 1992, there were high numbers of *S. benedicti* in the surface sediment at NCC and NCD (5,000 m^2^ and 11,500 m^2^, respectively) (Fig. 3), but there was very little biomass (3.46 g m^2^ at NCC and 1.15 g m^2^ at NCD) (Fig. 4). Station NCD had a large number of *r*-selected species in April 1993 when oligochaetes numbered 4,000 m^2^, but there was no *M. ambiseta* found in the samples at that time. There are three possibilities for these observations. (1) There may have been a species recruitment event in those areas, (2) there may have been a local disturbance, e.g., that caused by a shrimp trawl, or (3) perhaps there was sampling error, i.e., *S. benedicti* may be there constantly, but only in a localized area that was never sampled again. *Streblospio benedicti* was an abundant polychaete on occasion at some of the stations in past studies (Flint et al. 1980; 1983). Since large numbers of any of these pioneering species were not consistently encountered, there is no evidence that La Quinta Channel is a disturbed environment.

The dominance of deeper-dwelling organisms, e.g., *M. ambiseta*, and the low numbers of pioneering species indicates that Corpus Christi Bay and La Quinta Channel were not disturbed in the short time before each
sampling period. However, it would be incorrect to state that there had never been a disturbance in these areas. The sampling in Corpus Christi Bay, which was the reference area, took place in areas with little or no anthropogenic influences (i.e. dredging or sewage release) (pers. comm., M. E. Vega, Texas Parks and Wildlife Department). No visible anthropogenic influences, such as trawling or boating, were witnessed in the shoal areas of the La Quinta Channel, either, but they could have occurred. The sampling period took place during a wet year. According to Kalke & Montagna (1991), benthos survive better during wet years. Lastly, no dredging occurred in the La Quinta Channel during the study period (the last dredging occurred during early to mid 1991). With these caveats in mind, the present data reflects a lack of disturbance at all stations studied in La Quinta Channel.

When an area is not disturbed, the benthic diversity will be high. Conversely, if an area is disturbed, the diversity will be low (Rhoads et al. 1978). Diversity was high at every station except for station NCD. Using H', the mean overall diversity at the La Quinta Channel stations was 2.45 and the Corpus Christi Bay stations was 1.99. The Bay stations without NCD had a diversity index of 2.32. Measures of species diversity (H') in previous studies of the La Quinta Channel averaged 1.74 (Holland et al. 1974), 1.83 (Holland et al. 1975), 3.76 (Flint et al. 1980; Flint & Younk 1986), and 3.49 (Flint et al. 1983). Corpus Christi Bay averaged 2.89 (Holland et al. 1974), 3.26 (Holland et al. 1975), 1.63 (Flint et al. 1983), and 2.41 (Montagna & Kalke 1992). The diversity indices for this study were within the mid-range of past studies of the study areas, again supporting the conclusion that La Quinta Channel does not show signs of disturbance.

The average abundance and biomass to a depth of 10 cm during this study period are similar to those of previous studies. There was an average of 22,470 individuals m⁻² and 13.8 g m⁻² in the La Quinta Channel stations and 20,128 individuals m⁻² and 9.8 g m⁻² for Corpus Christi Bay stations (Table 1). The numbers of individuals found in La Quinta Channel in previous studies (Flint et al. 1980; Flint & Younk 1983; Flint et al. 1983) were much lower, averaging 9,000 individuals m⁻². The most likely reason for the difference is interannual variability. However, Flint also used a Peterson grab for sampling, which can underestimates benthic abundance, since it does not take an even sample like a core. Flint measured wet weight biomass and is not comparable to the data reported here (in Table 1). The numbers of individuals found in Corpus Christi Bay by Montagna & Kalke (1992) averaged
20,000 individuals m\(^{-2}\) and only 4.4 g m\(^{-2}\). Even though the numbers of individuals m\(^{-2}\) was the same between the two studies, our biomass was higher because NCC had ophiuroids throughout the sampling period, adding about 4 g m\(^{-2}\) to the total. No ophiuroids were reported by Montagna & Kalke (1992). In general, the current findings are comparable mostly to Montagna & Kalke (1992), who used the same techniques.

Heavy metals and pesticides accumulate in sediments and in bottom organisms where their concentrations increase (Karpinsky 1992). Sediment was analyzed for trace metals, volatile organics, and extractable organics by AnalySys, Inc. (1993). After comparing the levels of trace metals with a study by Long & Morgan (1991), all of the trace metals were considered to be in the "no effect" range. Other studies in Ingleside Cove (near LQB) examined concentrations of pollutants in the oyster *Crassostrea virginica* (Presley et al. 1990; Sericano et al. 1990; Garcia-Romero et al. 1993; Sericano et al. 1993). Pesticides, including DDT and non-DDT, PCB's, and chlordane-related pesticides, were at or below the averages found along the Texas coast. The pesticide DDT was found at levels of less than 1 ng g\(^{-1}\) dry weight, the non-DDT pesticides were found at levels of 1 ng g\(^{-1}\) dry weight, and PCB's were measured to be less than 10 ng g\(^{-1}\) dry weight (Sericano et al. 1990). The chlordane-related pesticides averaged 8.89 ng g\(^{-1}\) dry weight (Sericano et al. 1993). Garcia-Romero et al. (1993) conducted a study on butylized species of elemental tin (Sn) along the Texas coast. They determined that in Corpus Christi Bay an anti-fouling paint (Tributyltin) and its degradants were above average for the Texas coast with 200 ng Sn g\(^{-1}\) for tributyltin, 75 ng Sn g\(^{-1}\) for dibutyltin, and 30 ng Sn g\(^{-1}\) for monobutyltin. Presley et al. (1990) calculated that oysters accumulated 100 ppb of mercury in the Ingleside Cove area, which was lower than average for the Texas coast. La Quinta Channel, which has some pollution in it, appears to be as clean or cleaner than most bays along the Texas coast.

Channels bear maritime traffic and require maintenance. There was dredging in Corpus Christi Bay from February 1992 to June 1992 (R. Beggs at Corps of Engineers, Corpus Christi, pers. comm.). Dredging started from the junction of the La Quinta Channel and the Corpus Christi Ship Channel to Beacon 82 (1.6 km east of Harbor Bridge). There has been no dredging in the La Quinta Channel since July 1991. During 1992, there were 1,011 ships with drafts of greater than 10 m that traversed the Inner Channel (part of the Corpus Christi Ship
Channel) and 179 of those used the La Quinta Channel (Port of Corpus Christi, pers. comm.). During 1993, 1,124 ships used the Inner Channel and 124 of those used the La Quinta Channel. While shrimp boat traffic has been witnessed during each of the sampling periods, we have no information about how much traffic was present during the study year or which specific areas were trawled. The presence of mature stage macrobenthos in La Quinta Channel supports the idea that, while La Quinta Channel may undergo short-term disturbances due to maritime traffic and dredging, the channel area can recover within a few years.

Throughout the study period, both the La Quinta Channel and Corpus Christi Bay stations had similar benthic diversity, abundance, biomass and community structure. During the study, there was little evidence that disturbances had recently occurred, except for the minor ones previously mentioned at NCC and NCD. Based on an analysis of the data from the present study and a comparison with data from previous studies within Corpus Christi Bay, there is no evidence that the stations sampled in La Quinta Channel are less healthy or more disturbed than the stations sampled in Corpus Christi Bay. In fact, it appears that the reference station NCD in Corpus Christi Bay was the only station exhibiting characteristics of a degraded environment. Studies on a longer time scale, or with greater spatial resolution, or on the ecosystem level may be needed to determine the health of the entire system with certainty.

Acknowledgments

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This project was partially supported by the Coastal Bend Bays Foundation (CBBF). The CBBF, Occidental Chemical Company, and the Texas Natural Resource Conservation Commission worked cooperatively to support this study. Partial support was also provided by the University of Texas Marine Science Institute, and by Institutional Grant NA16RG0445-01 to Texas A&M University Sea Grant Program from the National Sea Grant Office, National Oceanic and Atmospheric Administration, U.S. Department of Commerce. University of Texas Marine Science Institute Contribution number 945.
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CELL WALL DEGRADING ENZYMES PRODUCED BY THE PHYTOPATHOGENIC FUNGUS PHYMATOTRICHUM OMNIVORUM

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Abstract.—The extracellular plant cell wall degrading enzymes of Phymatotrichum omnivorum and the effect of different carbon sources on the production of these enzymes were investigated. Cellobiohydrolase, endoglucanase and xylanase activities were detected in fluids collected from cultures containing sodium carboxymethyl cellulose (CMC) or xylan as carbon sources and enzyme inducers. The highest activities of cellobiohydrolase and xylanase were measured in fluids collected from cultures containing xylan. Results of this study indicate that P. omnivorum constitutively produces small amounts of endoglucanase.

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

Phymatotrichum omnivorum attacks many field crop plants of economic importance. It causes root rot of alfalfa, cotton, peanuts, soybeans, sugarbeets (Nywall 1989) and sweetpotatoes (Cook 1978). This pathogen also causes root rots of ornamental plants such as abelia, acacia, cedar, california poppy, privet, lobelia and many others (Pirone 1978).

The primary objectives of this study were to determine the components of extracellular plant cell wall degrading enzymes of P. omnivorum and to determine the effects of the carbon source on the production of these enzymes by P. omnivorum.

Materials and Methods

Organism and culture conditions.—Stock cultures of P. omnivorum were maintained on PDA slants (Difco, B13). The fungus was previously grown in 250 ml flasks with 125 ml of a medium containing: 0.02% MgSO₄·7H₂O, 0.01% Ca(NO₃)₂·4H₂O, 0.1% Peptone, 0.2% yeast extract, 2.0% glucose in sodium citrate buffer at pH 5.0. After four days growth at 26°C, five ml of mycelium inoculum was washed
twice in distilled water and then transferred to the cellulolytic growth medium. The medium for the production of cellulases contained: 0.25% NH₄NO₃, 0.10% K₂PO₄, 0.05% MgSO₄, 0.05% Ca(NO₃)₂·4H₂O, 0.72 ppm Fe(NO₃)₃·9H₂O, 0.44 ppm ZnSO₄·7H₂O, 2.0 ppm MnSO₄·4H₂O, 0.40 ppm ZnCl₂, and 0.8% carbohydrate. The carbohydrates used as carbon sources and enzyme inducers were: sodium carboxymethyl cellulose (CMC, type 7HF, Aqualon Company), microcrystalline cellulose and xylan (Sigma Chemical Company). Control cultures had glucose as the sole carbon source. The pH of the growing medium was adjusted to 5.0 with 0.1N KOH. Incubation of the cultures was carried out for eight days in covered 250 ml flasks on an orbital shaker at 80 rpm and 26°C.

Enzyme preparation and assays.—Culture fluids were collected after eight days of growth by centrifugation (4800 rpm, 20 minutes, 10°C). The supernatant was subsequently used for the determination of extracellular enzyme activity. For simplification, the collected supernatant is hereafter referred to as the enzyme. All tests were replicated four times.

Cellobiohydrolase (1,4-B-D-glucan cellobiohydrolase, EC 3.2.1.91).—Cellobiohydrolase activity was measured by combining one ml of enzyme with 25 mg of microcrystalline cellulose in one ml of 0.05 M sodium citrate buffer (pH 5.0) and incubating the reaction mixture for two hours at 40°C. The tubes were stirred several times during incubation. After centrifugation, the concentration of reducing sugar in the supernatant was determined using the dinitrosalicylic acid reagent (Miller 1959).

Endoglucanase (CM-cellulase, carboxymethyl cellulase, EC 3.2.1.4).—Endoglucanase activity was measured by combining one ml of enzyme with 10 mg of carboxymethyl cellulose in two ml of 0.05 M sodium citrate buffer (pH 5.0). The reaction mixture was incubated at 40°C for two hours. The concentration of reducing sugar in the reaction mixture was determined using the dinitrosalicylic acid reagent (Miller 1959).

Xylanase (EC 3.2.1.32).—Xylanase activity was measured by combining 10 mg of xylan in one ml of 0.05 M sodium citrate buffer, pH 5.0, with one ml of enzyme. The reaction mixture was incubated at 40°C for two hours. After centrifugation, the concentration of reducing sugars in the supernatant fluid were determined using the dinitrosalicylic acid reagent (Miller 1959).
Table 1. Effect of different carbon sources on the specific activities \(^1\) of extracellular cell wall degrading enzymes produced by *Phymatotrichum omnivorum*.

<table>
<thead>
<tr>
<th>Carbon source</th>
<th>Cellobiohydrolase</th>
<th>Endoglucanase</th>
<th>Xylanase</th>
<th>Extracellular protein (^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microcrystalline cellulose</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.22 ± 0.50</td>
</tr>
<tr>
<td>CMC</td>
<td>8.48 ± 0.13</td>
<td>15.36 ± 0.53</td>
<td>22.72 ± 0.38</td>
<td>0.64 ± 1.08</td>
</tr>
<tr>
<td>Xylan</td>
<td>48.67 ± 2.36 (^*)</td>
<td>26.57 ± 0.20</td>
<td>265.91 ± 5.17 (^*)</td>
<td>1.49 ± 0.66 (^*)</td>
</tr>
<tr>
<td>Glucose</td>
<td>0.0</td>
<td>73.06 ± 5.68 (^*)</td>
<td>0.0</td>
<td>0.28 ± 0.63</td>
</tr>
</tbody>
</table>

\(^1\) \(\mu\)M of glucose or its reducing sugar equivalent/min/ml/mg of protein. Means ± SD of four replications.
\(^2\) mg/ml.
\(^*\) Using one-way ANOVA and Duncan’s MRT, significantly different from other values in the same group.

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

**Data analysis.**—The results were expressed as units of specific enzyme activity and represent means plus or minus the standard deviation of four replications. One unit of specific activity (Usp) was calculated as the amount of enzyme that liberated one micromole (\(\mu\)M) of glucose, xylose or their reducing sugar equivalents per minute per ml of enzyme per milligram of extracellular protein under the conditions of the assay. Statistical analyses of experimental data were made with one-way analysis of variance (ANOVA) and Duncan’s multiple range test (MRT).

Results

**Cellobiohydrolase.**—Production of cellobiohydrolase was induced in cultures that contained CMC and xylan. No cellobiohydrolase activity was detected in fluids collected from cultures with microcrystalline cellulose or glucose as the sole carbon source (Table 1). Maximum cellobiohydrolase specific activity (48.67 Usps, Table 1) was measured in fluids collected from cultures containing xylan. This activity was significantly higher (\(P = 0.05\)) than the cellobiohydrolase activities evaluated in fluids from cultures containing microcrystalline cellulose, CMC or glucose.
Endoglucanase.—Production of endoglucanase by *P. omnivorum* was detected in liquid cultures of the fungus containing CMC, xylan and glucose (Table 1). Maximum endoglucanase activity (73.06 Usp) was measured in culture fluids of the fungus grown in media containing glucose. This activity was significantly higher (*P = 0.05*) than the cellobiohydrolase activities evaluated in fluids from cultures containing microcrystalline cellulose, CMC or xylan (Table 1). Microcrystalline cellulose did not induce the production of endoglucanase in the cultures of *P. omnivorum* under the conditions of this study.

Xylanase.—Xylanase activities of *P. omnivorum* were detected in the fluids collected from cultures containing CMC and xylan. Maximum activity of this enzyme (265.91 Usp) was measured in fluids collected from cultures that had xylan as the sole carbon source (Table 1). This activity was significantly higher (*P = 0.05*) than the xylanase activities evaluated in fluids from cultures containing CMC, microcrystalline cellulose, or glucose; the latter two carbon sources did not induce the production of xylanase.

Discussion

Maximum production of cellobiohydrolase by *P. omnivorum* was measured in fluids from cultures containing xylan as enzyme inducer. Smaller amounts of this enzyme were measured in the fluids of cultures containing CMC. Similar results were obtained in other studies of the phytopathogenic fungi *Fusarium oxysporum* f. sp. *lycopersici* (cf. Ortega 1990) and *Exserohilum rostratum* (cf. Ortega 1993a). Although microcrystalline cellulose did not induce the production of cellobiohydrolase in cultures of *P. omnivorum*, previous reports indicate that this carbohydrate can induce cellobiohydrolase production in the plant pathogens *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *Alternaria brassicae* (cf. Ortega 1992), *E. rostratum* (cf. Ortega 1993a), and *Curvularia senegalensis* (cf. Ortega 1993b). Apparently, cellobiohydrolase was not constitutively produced by *P. omnivorum* under the conditions of this study. This was suggested by the absence of cellobiohydrolase activity in fluids collected from cultures containing glucose as the sole carbon source. However, other plant pathogens, such as *A. brassicae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993) seem capable of producing constitutively small amounts of this enzyme.

Endoglucanase production was induced in cultures containing CMC or xylan as carbon sources. Similar results were obtained in other
studies of the phytopathogenic fungi *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *A. brassicae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993a). Endoglucanase was constitutively produced by *P. omnivorum* as indicated by the enzyme activity measured in fluids from cultures with glucose as the sole carbon source. The endoglucanase activity produced constitutively was significantly higher than the enzyme activity that was induced by CMC or xylan. This enzyme is also produced in a constitutive manner by the plant pathogenic fungi *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *A. brassicae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993a).

Maximum xylanase activity by *P. omnivorum* was detected in fluids from cultures with xylan as the carbon source and enzyme inducer. Similar results were obtained in studies of the phytopathogenic fungi *F. oxysporum* f. sp. *lycopersici* (cf. Ortega 1990), *A. brassicae* (cf. Ortega 1992) and *E. rostratum* (cf. Ortega 1993a). *P. omnivorum* did not produce xylanase constitutively. Other reports indicate that the phytopathogenic fungi *Rhizoctonia solani* (cf. Robson et al. 1989) and *E. rostratum* (cf. Ortega 1993a) do produce small amounts of xylanase in a constitutive manner.

Production of the cell wall degrading enzymes cellobiohydrolase, endoglucanase and xylanase was induced in liquid cultures of *P. omnivorum* when CMC or xylan were used as sole carbon sources. Xylanase activities were significantly higher than the activities of the enzymes cellobiohydrolase or endoglucanase. The most effective xylanase inducer was xylan.

**Literature Cited**


GENERAL NOTES

THE EASTERN PIPISTRELLE, *Pipistrellus subflavus* (CHIROPTERA: VESPERTILIONIDAE), FROM THE BIG BEND REGION OF TEXAS

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The eastern pipistrelle, *Pipistrellus subflavus* (F. Cuvier), has been reported in Texas to occur as far west as Lubbock County in the north (Jones et al. 1993), Irion and Tom Green counties in the central part of the state (Dowler et al. 1992), and Val Verde County in the south (Schmidly 1991). The species was recorded from Coahuila, Mexico (Baker 1956), but it has not been documented to occur in Chihuahua, Mexico (Anderson 1972).

This report represents the first record of the eastern pipistrelle from the Big Bend region of West Texas. A single specimen of *P. subflavus* was collected in the Big Bend Ranch State Natural Area, UTM coordinates 13 576658E, 3296469N (approximately 32 km N, 16 km E of Presidio, Presidio County, Texas). The specimen, an adult male (testes = 4 by 2 mm), was collected at 0430 hrs on 8 July 1994 in a mist net placed across a small stream. The stream is bordered by well-developed riparian vegetation consisting of dominant plants, such as *Salix* sp., *Baccharis* sp., and *Populus* sp. Adjacent to the stream and riparian area, the vegetation includes typical plants of the Chihuahuan Desert, such as *Prosopis* sp., *Larrea* sp., *Acacia* sp. and *Fouquieria* sp. Other bats taken in the area from 5-8 July included *Myotis velifer*, *Eptesicus fuscus*, *Plecotus townsendii* and *Antrozous pallidus*. In addition, *Pipistrellus hesperus* was observed flying about each evening. Based on observations and collections, it appears that *P. hesperus* represents the most common bat at the locality along the stream and in riparian vegetation where *P. subflavus* was collected.

Sympatry of *P. subflavus* and *P. hesperus* in West Texas was mentioned by Dowler et al. (1992) and indicated by Schmidly (1991). Both species of pipistrelles are present in Coahuila, Mexico, but were not found to occur together (Baker 1956). Relatively complete
ecological separation of these species in Coahuila was discussed by Baker (1956), who suggested that the eastern pipistrelle frequented forested streams, whereas the western pipistrelle apparently was most common in arid desert plains and mountainous areas. Baker (1956) also discussed the possible dispersal route of the eastern pipistrelle westward to Coahuila and elsewhere by way of the Rio Grande valley. Given the overlaps in the geographic ranges of these species in Texas, it appears that opportunities exist for studies of the ecological relationships of these two pipistrelles.

Based primarily upon size, the specimen of *P. subflavus* reported herein is tentatively assigned to *P. subflavus clarus* Baker. However, it must be noted that the color of the pelage of this specimen is not as pale as that described for and observed in specimens of *P. subflavus clarus*. Additional specimens are required in order to clarify the systematic affinities of these bats in West Texas.

Voucher materials, skin and skull (TTU 67145) and frozen tissues (TK 41846), are deposited in the Collection of Recent Mammals in the Natural Science Research Laboratory of the Museum of Texas Tech University.

Specimens were collected from the Big Bend Ranch State Natural Area in accordance with scientific collecting permits issued by the Texas Parks and Wildlife Department (permit numbers SPR-0790-189 and 4-94). Financial assistance was provided by the Natural Resources Program (David H. Riskind, Director) of the Texas Parks and Wildlife Department. Logistic support was provided by personnel of the Big Bend Ranch State Natural Area (Luis Armendariz, Superintendent). Mary Ann Abbey provided assistance in the collection and preparation of specimens in the field.

Literature Cited

NOTEWORTHY RECORDS OF AMPHIBIANS AND REPTILES FROM NORTHWESTERN AND WESTERN TEXAS

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This study was done in conjunction with field studies conducted on small mammals in the panhandle and western areas of Texas. All specimens reported in this study represent county records as interpreted from the distribution maps of Dixon (1987). Scientific and common names follow those of Dixon (1987) and Collins (1990). Included are records of six species of amphibians, one turtle, one lizard and 11 snakes. Voucher specimens are deposited with the holdings of The Museum at Texas Tech University (TTU).

Spea multiplicata (Cope)  
(New Mexico Spadefoot Toad)

Material examined.—Wolf Creek, 9 mi E of Lipscomb, Lipscomb County, Texas, 24 July 1985, one specimen (TTU 11445). 8 mi S, 4 mi W of Whiteface, Cochran County, Texas, 30 May 1988, two specimens (TTU 11446-11447). 13 mi N, 12 mi E of Plains, Yoakum County, Texas, 9 July 1987, one specimen (TTU 11448). 6 mi NE of Monahans, Ward County, Texas, 22 May 1987, two specimens (TTU 11449-11450).

Bufo debilis debilis Girard  
(Eastern Green Toad)

Material examined.—Sonora, Sutton County, Texas, 19 September 1986, one specimen (TTU 11451) which was flooded from a ground squirrel (Spermophilus mexicanus) burrow.

Bufo debilis insidior Girard  
(Western Green Toad)

Material examined.—18 mi N, 1 mi W of Adrian, Oldham County.
Texas, 22 August 1985, one specimen (TTU 11452). 10 mi N, 35 mi W of Hereford, Deaf Smith County, Texas, 17 August 1989, one specimen (TTU 11453).

*Bufo punctatus* Baird & Girard
(But-red-spotted Toad)

_Material examined._—Lake Meredith National Recreation Area, 1.5 mi S, 2.5 mi W of Fritch, Potter County, Texas, 17 August 1991, one specimen (TTU 11454). 7 mi S, 17 mi W of Clairemont, Kent County, Texas, 11 May 1993, one specimen (TTU 11455).

*Bufo speciosus* Girard
(Texas Toad)

_Material examined._—Wolf Creek, 9 mi E of Lipscomb, Lipscomb County, Texas, 24 July 1985, one specimen (TTU 11456). 7 mi W of Kermit, Winkler County, Texas, 5 August 1987, one specimen (TTU 11457).

*Rana catesbeiana* Shaw
(Bullfrog)

_Material examined._—Rita Blanco Creek, 1.5 mi S, 6 mi W of Channing, Hartley County, Texas, 10 June 1988, one specimen (TTU 11458). 3 mi S, 9 mi E of Justiceburg, Garza County, Texas, 10 June 1993, one specimen (TTU 11459); 4 mi S, 2 mi E of Justiceburg, Garza County, Texas, 18 April 1989, two specimens (TTU 11460-11461).

_Remarks._—When collected, the specimen from Rita Blanco Creek was in the process of consuming a cliff swallow (*Hirundo pyrrhonota*).

*Kinosternon flavescens flavescens* (Agassiz)
(Yellow Mud Turtle)

_Material examined._—7 mi N, 4 mi W of Notrees, Winkler County, Texas, 13 April 1989, two specimens (TTU 11462-11463).

*Eumeces obsoletus* (Baird & Girard)
(Great Plains Skink)

_Material examined._—3 mi E of Sylvester, Fisher County, Texas, 14 April 1991, one specimen (TTU 11464). 13.5 mi S, 0.5 mi W of Hamlin, Jones County, Texas, 14 April 1991, one specimen (TTU
11465). 13 mi N, 12 mi E of Plains, Yoakum County, Texas, 9 July 1987, one specimen (TTU 11466). 0.5 mi S, 11 mi W of Lees, Glasscock County, Texas, 6 June 1989, one specimen (TTU 11467).

**Remarks.**—Specimens were collected in Sherman live-traps which had been set for small mammals.

*Arizona elegans elegans* Kennicott
(Kansas Glossy Snake).

**Material examined.**—3.5 mi S of Muleshoe, Bailey County, Texas, 28 May 1988, one specimen (TTU 11468).

**Remarks.**—The specimen was collected in sand hills habitat north of the Muleshoe National Wildlife Refuge.

*Coluber constrictor flaviventris* Say
(Eastern Yellowbelly Racer)

**Material examined.**—3 mi N, 8 mi W of Spur, Dickens County, Texas, 7 June 1987, one specimen (TTU 11469).

*Diadophis punctatus amyli* Kennicott
(Prairie Ringneck Snake)

**Material examined.**—10 mi S, 15 mi E of Spearman, Roberts County, Texas, 16 May 1988, one specimen (TTU 11470).

*Elaphe guttata emoryi* (Baird & Girard)
(Great Plains Rat Snake)

**Material examined.**—7.5 mi E of Lutie, Collingsworth County, Texas, 14 May 1986, one specimen (TTU 11471). 3 mi S of Floydada, Floyd County, Texas, 4 September 1989, one specimen (TTU 11472).

*Elaphe obsoleta lindheimeri* (Baird & Girard)
(Texas Rat Snake)

**Material examined.**—12 mi E of Canadian, 20 July 1984, one specimen (TTU 11473); 1.5 mi N, 13 mi E of Canadian, Hemphill County, Texas, 25 May 1985, one specimen (TTU 11474).

**Remarks.**—These are the first records of this species from the Texas Panhandle.
Lampropeltis getula splendida (Baird & Girard)
(Desert Kingsnake)

Material examined.—3.5 mi W of Best, Reagan County, Texas, 1 July 1986, one specimen (TTU 11475). 8 mi S of Whiteface, Cochran County, Texas, 30 May 1988, one specimen (TTU 11476).

Lampropeltis triangulum celaenops Stejneger
(New Mexico Milk Snake)

Material examined.—13 mi S of Lehman, Cochran County, Texas, 15 August 1988, one specimen (TTU 11477).

Remarks.—This specimen was collected in a Sherman live-trap in an area of sandy soils and shinoak.

Rhinocheilus lecontei tessellatus Garman
(Texas Longnose Snake)

Material examined.—6 mi N of Fieldton, Lamb County, Texas, 2 June 1988, one specimen (TTU 11478).

Remarks.—This specimen was collected in the Muleshoe Sand Hills of northwestern Texas.

Tantilla hobartsmithi Taylor
(Southwestern Blackhead Snake)

Material examined.—McCamey, Upton County, Texas, 6 June 1986, one specimen (TTU 11479).

Thamnophis radix haydeni (Kennicott)
(Western Plains Garter Snake)

Material examined.—16 mi S, 11 mi E of Spearman, Roberts County, Texas, 16 May 1988, one specimen (TTU 11480).

Agkistrodon contortrix pictigaster (Gloyd & Conant)
(Trans-Pecos Copperhead)

Material examined.—4 mi S, 2 mi E of Crane, Crane County, Texas, 24 July 1986, one specimen (TTU 11481).
OBSERVATIONS OF WINTERING FERRUGINOUS HAWKS
(Buteo regalis) FEEDING ON PRAIRIE DOGS
(Cynomys ludovicianus) IN THE TEXAS PANHANDLE

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Ferruginous hawks (Buteo regalis) winter in Texas from the Southern High Plains southwest into the Big Bend region and adjacent northern Mexico (Schmutz & Fyfe 1987; Palmer 1988; Johnsgard 1990; Olendorff 1993). They commonly occur in areas of cultivation but small groups are often observed in association with remnant prairie dog (Cynomys ludovicianus) towns in patches of over-grazed native short-grass prairie. They perch on shrubs or on the ground either in or near the perimeter of towns. Hawks perched on the ground are largely ignored by the prairie dogs (Palmer 1988). While the importance of prairie dogs in this hawk’s diet appears apparent, there have been few accounts describing the manner in which prairie dogs are captured and consumed by ferruginous hawks (Olendorff 1993). This report describes the foraging and feeding behavior of ferruginous hawks on prairie dogs in the Texas Panhandle.

On the morning of 9 January 1995, four ferruginous hawks and an adult bald eagle (Haliaeetus leucocephalus) were observed at a 450-acre area of native short-grass prairie habitat east of Amarillo, Texas, which supports a large prairie dog town. The hawks were perched on the ground and on utility structures in and adjacent to the prairie dog town. The eagle was soaring overhead. At approximately 1100 hr, one of the ground perched hawks captured a prairie dog, the hawk hopping on the ground and flapping its wings as it struggled with its prey. Its struggle immediately drew the attention of the other three hawks and within a few minutes nine more ferruginous hawks and one rough-legged hawk
(Buteo lagopus) had surrounded the first hawk in a close group on the ground. Both adult and immature ferruginous hawks were among the group (most were immature). The new arrivals flew to the capture site very fast and just a few meters above the ground. They showed little hesitation in joining the group and began bumping and nudging one another in a form of "feeding frenzy" not previously reported for this species. Several hawks attempted to steal the prey during the frenzy. This was followed by considerable hopping, flapping, and fighting as several different individuals stole the prairie dog, mantled it, and fed upon it. The adult eagle flew over the area twice but did not join the group. Within 10 minutes, presumably after the prey had been consumed, the group dispersed and disappeared into the short-grass prairie landscape.

Later that morning, at approximately 1200 hr, a similar feeding frenzy took place in the same area. On this occasion, 11 ferruginous hawks (again mostly immature) assembled and fought over the prey. This time the adult eagle swooped down into the group and stole the prey, remaining in the group to eat the prey. Although a few hawks remained within the vicinity for a short time, most of them dispersed immediately after the eagle took the prey.

On 10 January 1995, at 1640 hr, a third feeding frenzy was observed. Eleven ferruginous hawks, most immature, again gathered around a single ferruginous hawk that had just captured a prairie dog, and several birds fought over the prey. Here, too, the group disbanded within 10 minutes after the prey had been caught and then exchanged among four or five hawks. No other species were observed taking part in the feeding activities.

Chesser (1979) reported a colony of wintering ferruginous hawks in New Mexico that was attracted by the shooting of prairie dogs. The group appeared regularly when shooting began and followed the vehicle used by the hunters, apparently associating gunfire with easily obtainable prey. A similar occurrence was observed on 8 January 1995, when a .22 caliber rifle was used to shoot prairie dogs for use as bait to trap ferruginous hawks west of Amarillo, Texas. After only a few shots were fired, a group of six ferruginous hawks had circled and perched on the ground nearby. When a 20 gauge shotgun was fired, one hawk immediately flew over the target mound. Harmata (1981) and Gilmer et al. (1985) listed shooting as a common cause of death for ferruginous hawks. Their apparent attraction to locations where prairie dogs are being hunted may be one reason that these birds are often shot.
Acknowledgments

We thank the U.S. Department of Energy, Mason and Hanger—Silas-Mason Co., Inc., and Battelle Pantex for partial support of this project under Contract FPR000049. We also thank J. C. Cepeda and Laurel Grove for reviewing this manuscript.

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THE RODENT COMMUNITY AND ASSOCIATED VEGETATION IN A TALLGRASS BLACKLAND PRAIRIE IN TEXAS

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Abstract.—This study reports the first systematically collected data on the small mammal community in both undisturbed and disturbed tracts of a remnant Blackland Prairie in Hunt County, Texas. During three years of seasonal study, the two principal habitats (grassland and wooded draw) were sampled using mark-release-recapture methods. Peromyscus leucopus, Peromyscus maniculatus and Sigmodon hispidus occurred in both habitats. Reithrodontomys fulvescens and Reithrodontomys humulis occurred only in the grassland, whereas Neotoma floridana was trapped only in the wooded draw. Mus musculus was found in disturbed areas away from the trapping grids. Estimates of population densities and longevity are provided for several of these species of rodents. Quantitative data on vegetative cover characterizing grassland and wooded-draw habitats is also provided. The composition of the rodent fauna is considered biogeographically.

The tallgrass Blackland Prairie of east-central Texas is well-studied floristically, but its small mammal fauna has not been well-characterized. It is one of approximately 10 major physiognomic regions in Texas (Tharp 1939; Gould 1975) and emerged as a distinct floral association in postglacial times approximately 10,000 YBP (Gehlbach 1991). In its former undisturbed condition, the Blackland Prairie in Texas extended from near the Red River in northeastern and north-central Texas southward along the eastern edge of the Balcones Escarpment to its termination near San Antonio. The blacklands represent an ecotone between the oak-hickory and pine forests to the east and the Cross Timbers, Grand Prairie, and Edwards Plateau regions to the west. Prior to its colonization by non-native humans during the middle-to-late 1800's, the Blackland Prairie comprised some 4.3 million hectares of grassland and associated habitats; presently, as little as only 4,000 ha of unbroken sod remains (Diamond & Smeins 1993).

The flora of the Blackland Prairie has been well characterized (Smeins & Diamond 1983; Diamond & Smeins 1985; 1993) in comparison to its fauna. To date, only one published paper treats the wildlife diversity of the Blackland Prairie (Schmidly et al. 1993), though several papers indirectly address the mammalian fauna of this region. Bailey (1905:19) recognized the Blackland Prairie and the adjacent Grand Prairie to the west as ecosystems to which few if any species of mammals were restricted. Biogeographically, the Blackland Prairie (as part of Blair’s...
Texan biotic province) has greater significance as a region where eastern species reach western limits of range and western species attain their eastern range limits (Blair 1950). Strecker (1924; 1926) published annotated checklists of the mammals of McLennan County, which straddles the transition of habitats from Blackland Prairie in the eastern sections of the county to other assorted ecosystems to the west; these papers offer limited insight regarding certain mammals of this county when considerable undisturbed habitat still remained. In other treatments of the mammalian fauna of eastern Texas, McCarley (1959) excluded the Blackland Prairie in his definition of eastern Texas, whereas Schmidly (1983) recognized the Blackland Prairie as the westernmost segment of eastern Texas. The bat fauna of Texas east of the blacklands was reported by Schmidly et al. (1977). All other published reports on mammals from eastern Texas and the blacklands have pertained to the biology of individual species or groups of species in restricted areas.

This paper reports the results of a three-year study of the small mammal community of the largest remnant of undisturbed tallgrass prairie in the Blackland Prairie of Texas. The Clymer Meadow preserve, located approximately 5 km west of Celeste in Hunt County, is an approximately 126 ha remnant of tallgrass prairie owned by the Nature Conservancy of Texas. Because much of the Clymer preserve is a remnant of natural habitat, it is reasonable to expect the rodent fauna to include the full diversity of native species adapted to the habitats present on the preserve. The population abundances and other natural history information obtained for these species may, therefore, more closely approach "natural values" than do such data obtained from non-native and disturbed habitats in the same area. Vegetative cover was also studied because the "general composition of small mammal communities in different types of grasslands appears to be determined primarily by structural attributes of the habitat" (Grant et al. 1985:589). The objectives of the study were (1) to develop an inventory of the small mammal species on the preserve, (2) to obtain information on population dynamics of small mammal species (i.e., rodents) present in different disturbed and undisturbed habitats, and (3) to assess relationships of vegetation and plant cover to distribution of small mammal species in native undisturbed prairie.

Study Area

The terrain at Clymer Meadow is rolling, with grassland on slopes and many hilltops and with woodland in draws and on some hilltops.
Soil is a deep, black clay having considerable shrink-swell capacities. Property adjacent to the preserve is variously grazed, farmed, and used for production of native hay. Most of the property on the preserve historically has served as hay meadows, and some has been grazed, but with the exception of a small garden plot adjacent to a house, none has been plowed and cultivated.

Though the grassland component of the Blackland Prairie is structurally rather homogeneous, the particular plant species comprising the grassland vary regionally on the basis of soils and other features, such that different “series” of grassland communities are recognized. Clymer Meadow exemplifies the “little bluestem (Schizachyrium scoparium)-Indiangrass (Sorghastrum nutans) series” (Diamond & Smeins 1985). Occurring with these dominant species are several other native grasses: switchgrass (Panicum virgatum), eastern gamagrass (Tripsacum dactyloides), big bluestem (Andropogon gerardii), tall dropseed (Sporobolus asper), side oats grama (Bouteloua curtipendula), Florida paspalum (Paspalum floridanum), Scribner panicum (Dicanthelium oligosanthes), Texas wintergrass (Stipa leucotricha), and fimbry (Fimbristylis puberula). A diverse array of forbs is present.

Native woodland characterizes the drainages of Clymer Meadow. The principal species of trees are cedar elm (Ulmus crassifolia), bois d’arc (Maclura pomifera), and Texas sugarberry (Celtis laevigata). The primary woody species in the understory are coralberry (Symphoricarpos orbiculatus), roughleaf dogwood (Cornus drummondii), and poison ivy (Toxicodendron radicans); very little of the ground surface is covered by forbs or grasses. Water flow in these draws is intermittent, with timing and amount of water related to pattern and amount of precipitation. Mottes of woody vegetation, surrounded by grassland, occur sporadically on the hillsides and hilltops. Generally, such a motte consists of a central bois d’arc or sugarberry tree beneath which is a thicket of poison ivy and coralberry.

Methods and Materials

Grid studies.—Population densities of small mammals were determined by analyzing mark-recapture data obtained from live-trapping on grids and transects (Blair 1941; Hayne 1949). The method used to estimate population sizes was based on the minimum number of different individuals handled during a sampling session; this method is almost always an underestimate of population size (Overton 1972).
Two trapping grids were established on the Parkhill tract of Clymer Meadow to sample rodents in the two primary terrestrial habitats representative of tallgrass prairies. One grid, the grassland grid, sampled unperturbed prairie. The other, the wooded-draw grid, sampled the wooded habitat characteristic of lower elevations and streambeds located between the higher, grassy hillsides and hilltops. These grids have been undisturbed by burning, grazing, or haying since before the Nature Conservancy of Texas acquired the property in 1986; prior to this, the only use of this tract was as a hay meadow. As such, the data from these grids represent a database useful in assessing effects of various perturbations of habitat.

The grassland trapping grid consisted of 50 trap stations arranged in a rectangular 5 by 10 array. The grid in the wooded draw consisted of three columns of 10 stations each for a total of 30 traps; the columns followed the contours of the draw. Distance between adjacent trap stations in the same and adjacent rows was 15 m in the grassland grid and 10 m in the wooded-draw grid. The effective sampling areas of each grid consisted of the area within each grid plus the area of a boundary strip one-half the distance between traps (7.5 m wide for grassland grid; 5 m wide for wooded-draw grid; as per Blair 1942). Hence, the grassland and wooded-draw grids sampled 1.12 ha and 0.30 ha, respectively.

One Sherman livetrap (23 by 9 by 8 cm) was placed at each trap station on each grid. Trapping was conducted seasonally for 3 years, from April 1989 through January 1992. Spring, summer, fall, and winter sampling was conducted in April, July, October, and January, respectively. Each sampling session consisted of four consecutive days. Traps were placed, set, and baited with rolled oats on the afternoon of the first day, and were reset and rebaited on the afternoons of the second and third days. Traps were checked for presence of rodents and then closed soon after daybreak on the second, third, and fourth days. Closure of traps during daytime precluded mammals from entering traps during daytime.

For every rodent live-trapped, species identity, sex, age, reproductive condition, body weight, and trap station were recorded in the field prior to release at the site of capture. On occasion of first capture, each rodent was marked to enable future identification upon recapture. Marking was by toe-clipping (Wilkins 1977), a traditional method sanctioned by the American Society of Mammalogists (1987). Longevity for a particular species on a particular grid was determined by averaging
the lengths of time from first to last capture for each individual that was recaptured at least once.

**Vegetation analysis.**—Seasonal analysis of vegetative cover on each grid was conducted to assess relationships of quantity and type of vegetation to the rodent species present. A convenient method of canopy-cover analysis, modified from Daubenmire (1959), has worked effectively in other studies of small mammals (Wilkins 1977; Wilkins & Schmidly 1981) and was used as follows in this study:

Cover provided by 15 categories of plants was estimated at selected heights above the soil surface: litter at 5 cm; standing dead material at 10, 25, and 50 cm; big bluestem at 25 and 50 cm; switchgrass at 25 and 50 cm; other grasses at 25 and 50 cm; forbs at 5, 10, and 25 cm; and woody species at 50 cm and 1 m. Included in the "other grasses" category were many of the important species, such as little bluestem, indiangrass, and eastern gamagrass. Amount of cover provided was encoded as follows: 0 indicates 0%; 1, 1-5%; 2, 6-25%; 3, 26-50%; 4, 51-75%; 5, 76-95%, 6, 96-100%. The values used in computation are the midpoints of the respective ranges: code 1, 3%; 2, 15.5%; 3, 38% 4, 63%; 5, 85.5%; 6, 98%. Vegetative cover within a 0.2 by 0.5 m quadrat (area=0.1 m²) was assessed seasonally at the same 10 randomly selected trap stations in each grid during the 4-day interval when rodents were sampled. Statistical analysis of vegetation data was conducted by use of the MEANS and ANOVA procedures of the Statistical Analysis System (SAS Institute Inc. 1985).

**Sampling of small mammals away from grids.**—Additional sampling was conducted at Clymer Meadow beyond the locations and habitats represented on the grids. Sampling the other subhabitats present (disturbed grassland, grassland inhabited by fire ants, woodland, streamside, fencelines) allowed detection of species perhaps not occurring in the habitats represented by the grids and, thereby, facilitated a more-complete inventory for the preserve. Comparison of species compositions of rodent communities in different habitats allowed assessment of impact of various habitat perturbations.

Sherman live traps (baited with rolled oats) were placed in various subhabitats in transects of 30-40 stations (approximately 10 m apart) for one night. Information recorded was number of individuals of each species in the transect and, later in the study, the number of traps in which imported fire ants (*Solenopsis invicta*) were found. The vast majority of these rodents were released unharmed; the few animals pre-
Table 1. Summary statistics for rodent population densities (computed from minimum number known alive) on the grassland and wooded-draw sampling grids at Clymer Meadow, Hunt Co., Texas, 1989-1992. Listed are the means (and standard deviations) of number of rodents per hectare for each of six species averaged by season for the 3-year study period.

<table>
<thead>
<tr>
<th>Species</th>
<th>Grid and Season</th>
<th>S. hispidus</th>
<th>R. fulvescens</th>
<th>R. humulis</th>
<th>P. leucopus</th>
<th>P. maniculatus</th>
<th>N. floridana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>Spring</td>
<td>5.9 (2.8)</td>
<td>3.0 (3.7)</td>
<td>1.2 (1.0)</td>
<td>1.2 (1.4)</td>
<td>0.9 (0.9)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>16.7 (5.2)</td>
<td>2.7 (3.2)</td>
<td>0.9 (0.9)</td>
<td>1.2 (1.4)</td>
<td>0.6 (0.5)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>16.7 (4.1)</td>
<td>2.1 (1.9)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>12.8 (5.9)</td>
<td>4.5 (4.5)</td>
<td>0.0 (0.0)</td>
<td>0.3 (0.5)</td>
<td>0.3 (0.5)</td>
<td></td>
</tr>
<tr>
<td>Wooded-draw</td>
<td>Spring</td>
<td>0.0 (0.0)</td>
<td>32.2 (10.7)</td>
<td>23.3 (17.3)</td>
<td>3.3 (3.3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>0.0 (0.0)</td>
<td>24.4 (18.4)</td>
<td>0.0 (0.0)</td>
<td>14.4 (6.9)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>1.1 (1.9)</td>
<td>16.6 (11.5)</td>
<td>4.4 (5.1)</td>
<td>4.4 (1.9)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>0.0 (0.0)</td>
<td>16.7 (12.0)</td>
<td>32.2 (18.4)</td>
<td>3.3 (3.3)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

pared as voucher specimens (deposited in the collection of vertebrates at Baylor University) generally were taken from these transects rather than from the grids.

Results

Population dynamics of grassland grid.—Five species of rodents, listed in order of decreasing abundance, were captured on the Parkhill grassland grid during 1,800 trapnights of sampling: *Sigmodon hispidus* (cotton rat; 153 different individuals), *Reithrodontomys fulvescens* (fulvous harvest mouse; 32 individuals), *Reithrodontomys humulis* (eastern harvest mouse, 7 individuals), *Peromyscus leucopus* (white-footed mouse; 7 individuals), and *Peromyscus maniculatus* (deer mouse; 7 individuals).

*Sigmodon hispidus* was the only species caught every sampling session; densities based on minimum number of different individuals present ranged from 2.7/ha to 21.4/ha (Table 1). For each year of the study, springtime densities of *Sigmodon hispidus* were lower than for any other season. Though none were handled during the first year of the study, *Reithrodontomys fulvescens* was trapped during each of the remaining eight sampling sessions; maximum density was 8.9/ha. Individuals of the other three species were captured only sporadically during the study; maximum densities for *Peromyscus leucopus*,
Peromyscus maniculatus, and Reithrodontomys humulis were estimated to be less than 3/ha throughout the study (Table 1).

Stick houses of eastern wood rats (Neotoma floridana) were constructed at the bases of woody mottes scattered over the grassland portions of the prairie. One such motte and nest was located at the northeastern corner of the grassland grid, yet no wood rats were caught there.

Longevity could not be assessed for Reithrodontomys humulis as none was ever recaptured. This species heretofore was unknown in Hunt County, Texas, thus two of the seven individuals were prepared as voucher specimens (Wilkins 1991). Three Peromyscus leucopus were recaptured, but all recaptures were during the same sampling session of their initial capture. Only one Peromyscus maniculatus was recaptured during a session later than its initial capture; the longevity of this male was at least 6 months. Nine different Reithrodontomys fulvescens were recaptured. Two were captured twice during the same session, four others were caught again during the next sampling session, one was recaptured 6 months after its first capture, another was recaptured 9 months after being marked, and one male was caught four times, the last occasion being 12 months after first capture. Mean minimum longevity computed from these nine multiply-captured Reithrodontomys fulvescens was 4.3 months, nearly twice the mean lifespan reported by Cameron (1977).

Sixty of 153 Sigmodon hispidus handled (39.2%) were recaptured at least once. The greatest longevity evident among these was 6 months (n=7). The last recapture for 21 cotton rats was 3 months after initial capture. For 32 individuals, all recaptures were during the same session that they were marked. On the basis of these 60 animals, mean minimum longevity for Sigmodon hispidus on this grid was 1.75 months, slightly shorter than values (2.0 - 2.6 months) summarized by Schmidly (1983).

Approximately 650 trapnights of effort were required for the initial capture of all five species of rodents that were caught on the grassland grid. Three species (Sigmodon hispidus, Peromyscus leucopus, Peromyscus maniculatus) were handled during the first sampling session of the first year of the project (i.e., during the first 150 trapnights). The first specimens of the fourth (Reithrodontomys fulvescens) and fifth species (Reithrodontomys humulis) were obtained during the first sampling session of the second year (i.e., after 650 trapnights).
Population dynamics of wooded-draw grid.—Sampling (1,080 trap-nights) indicated the presence of four species of rodents in the wooded-draw habitat. One of these species, *Sigmodon hispidus*, was represented by only one individual (density = 3.3/ha), a subadult caught one time near the ecotone of woods and grassland. Twenty different wood rats (*Neotoma floridana*) were trapped on this grid. Two other species were present in similar numbers: *Peromyscus leucopus* (*n*=52 individuals) and *Peromyscus maniculatus* (*n*=46). Densities of *Peromyscus leucopus* ranged from 3.3/ha to 40.0/ha (Table 1); those of *Peromyscus maniculatus* varied from 0/ha during four sessions to 33.3/ha (Table 1). A general trend evident for *Peromyscus maniculatus* is lower densities in summer and fall, and higher densities in winter and spring.

No *Neotoma floridana* were caught during the winter of year two or spring of year three, but they were present at densities of 3.3/ha to 20.0/ha during the rest of the study. For each year, their peak densities were during summer (Table 1). Fifteen of the 20 *Neotoma floridana* handled were never recaptured. Three of the remaining five were recaptured only within the session during which they were marked. The initial capture and recapture of one male spanned three seasons for a minimum longevity of six months. Another male was handled during spring of years one and two. Mean minimum longevity for *Neotoma floridana* as based on these five animals was 3.6 months.

Of the 52 *Peromyscus leucopus* captured, 21 (40.4%) were recaptured at least once. Four were recaptured only during their session of initial capture. The last record for seven more individuals was in the session immediately after session of first capture. Four others were captured two sessions after their original capture. Three were last captured in the third session following initial capture. Longevity in three others spanned four, six, and eight trapping sessions, respectively. Mean minimal longevity as based on these 52 mice was six months, more than three times the 1.7 month longevity determined by Waggoner (1975).

On this grid, mean minimal longevity for *Peromyscus maniculatus* was 2.1 months. Over one-third (37%, *n*=17) of the deer mice handled were recaptured one or more times. One male survived at least one year, being captured in consecutive winters. The trapping records for two other *Peromyscus maniculatus* spanned six months. Four others were last captured during the session immediately following the session of initial capture. Ten of the 17 recaptured individuals were recaptured only during the session of first capture.
The three species (*Peromyscus leucopus*, *Peromyscus maniculatus*, *Neotoma floridana*) constituting the vast majority of the rodent community of the wooded-draw habitat were initially sampled during the first sampling session of the first year of the study (i.e., within 90 trapnights). A fourth species (*Sigmodon hispidus*) was first trapped in this habitat after approximately 990 trapnights of effort, during the third session of the third year of the study.

**Vegetation analyses of grassland grid.**—Seasonal summaries of cover provided by 15 categories of vegetation are presented in Figure 1 and Table 2. The predominant grasses of the Blackland Prairie at Clymer Meadow are little bluestem and indiangrass. Indeed, these species in combination with the less-abundant switchgrass and eastern gamagrass offered the vast majority of vegetative cover on the grassland grid. Big
Table 2. Summary statistics for plant cover on the grassland and wooded-draw sampling grids at Clymer Meadow, Hunt Co., Texas, 1989-1992. Listed are the means and standard deviations (located below the mean) of percentage cover provided by each of 15 categories of vegetation averaged by season for the 3-year study period. Each mean was computed from 30 sampling quadrats each with an area of 0.1 m².

<table>
<thead>
<tr>
<th>Grid and Season</th>
<th>5 cm</th>
<th>10 cm</th>
<th>25 cm</th>
<th>50 cm</th>
<th>25 cm</th>
<th>50 cm</th>
<th>25 cm</th>
<th>50 cm</th>
<th>5 cm</th>
<th>10 cm</th>
<th>25 cm</th>
<th>50 cm</th>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>89.2</td>
<td>76.0</td>
<td>8.3</td>
<td>2.1</td>
<td>1.4</td>
<td>0</td>
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<td>1.4</td>
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<tr>
<td></td>
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<tr>
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<td>5.3</td>
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<td>16.1</td>
<td>23.7</td>
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<tr>
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<td>8.4</td>
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</tr>
<tr>
<td>Summer</td>
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<tr>
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<td>Winter</td>
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<td>0.7</td>
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bluestem did not contribute meaningfully to cover at any season, and that contributed by switchgrass never exceeded 10%. The greatest amount of grassy cover (as much as 41%) was provided by species in the "other grasses" category, primarily little bluestem, indiangrass, and eastern gamagrass. The amount of cover offered collectively by all grasses was far greater during summer (totalling slightly over 50% at 25 cm and nearly 15% at 50 cm) and fall (approximately 35% at 25 cm and nearly 10% at 50 cm) than during winter (<1% for all grass species at both heights) and spring (only about 5% for all grass species at both heights). Though woody vegetation was rare in native undisturbed grassland, it occurred in two situations: (1) in mottes, and (2) as seedlings and saplings of sugarberry, cedar elm, and mesquite (*Prosopis glandulosa*) growing amidst the grasses, especially in areas of greater soil moisture (e.g., in gilgai on the level hilltops and in drainage gullies along the slope). One such motte was located at the northwestern corner of the grid. Overall, however, the amount of cover provided by all types of woody vegetation combined was miniscule (<1%; Table 2).

The greatest amount of cover provided overall was by dead herbaceous material (i.e., litter or duff). For any particular season, litter closer to the ground provided more cover than did taller dead material. In all seasons, litter at 5 cm covered at least 50% of the ground surface, and litter at 10 cm always covered at least 33% of the surface. Dead material at 25 cm offered more coverage (24.6%) during winter than during any other season. The maximum value for dead material at 50 cm was only 3.5% (winter), and hence might be considered an unimportant component of plant cover. An array of forbs also was present, but during no season did forbs at any of the heights sampled offer more than 10% canopy coverage.

**Vegetation analyses of wooded-draw grid.**—Woody vegetation provided the vast majority of cover in the draw during all seasons, ranging from a minimum (5.6% at 50 cm and 23.9% at ≥1m) during winter when deciduous species had dropped their leaves to maxima for cover at 50 cm during spring (21.5%) and for cover at ≥1m during summer (70.8%; Table 2). During any season for any year, no category of dead herbaceous material contributed more than 14% cover. Litter in the woods most often was composed of fallen leaves of shrubs and trees rather than of stems and leaves of grasses as in the grassland.

Big bluestem, little bluestem, and switchgrass were absent from the wooded draw. Most of the grassy cover was provided by grasses in the "other grasses" category; the dominant grass was river oats
(Chasmanthium latifolium), occurring in areas devoid or nearly so of woody cover. As in the grassland grid, forbs were insignificant contributors to total vegetative cover. Maximum coverage by any category of forbs during any year of the study was 11.2% at 5 cm (during spring of year three) and 11.0% at 10 cm (during spring of year one). Herbaceous ground cover varied from virtually absent beneath a dense canopy to rather dense in light gaps.

Vegetation comparison of grassland and wooded-draw grids.—Cover on the two grids was provided by different groups of plants, with grasses and litter derived therefrom dominating on the grassland grid, and woody shrubs and trees dominating for the wooded-draw grid (Fig. 1). Analyses of variance were conducted to compare grids on the basis of amount of cover provided by each vegetation category for each season. For all four categories of dead herbaceous vegetation, the grids differed significantly ($P \leq 0.054$; d.f. = 59). Even more pronounced were the differences in cover provided by woody vegetation ($P \leq 0.0001$; d.f. = 59). Big bluestem and switchgrass, both absent from the wooded draw, provided only minor amounts of cover in the grassland. The amount of cover provided by “other grasses” was significantly greater in the grassland at 25 cm and 50 cm during fall ($P \leq 0.0515$; d.f. = 59) and at 25 cm during summer ($P \leq 0.0001$; d.f. = 59); during other seasons at both 25 cm and 50 cm, amount of cover provided by “other grasses” was similar. Values for cover provided by the various categories of forbs for both grids hovered at or below 10% for all seasons. Forbs at 25 cm offered significantly greater amounts of cover in the grassland (8.3% vs. 0.4% in wooded draw) during summer ($P \leq 0.008$; d.f. = 59). During fall, cover from forbs at 10 cm and 25 cm was significantly greater in the grassland ($P \leq 0.0030$; d.f. = 59); probably these values are not biologically meaningful as the range in these cover values was 0.1% to 3.1%. Care must be taken in comparing the forbs and the “other grasses” categories between grids because these categories comprised different species in the two habitats being compared.

Additional small mammal sampling.—Beyond sampling on the trapping grids, 1,653 additional trapnights of effort were invested in other areas of the preserve having different land uses (Table 3). During the 3-year study, 167 rodents of five species were livetrapped away from the grids for a trapping efficiency of 10.1%. Sampling in the disturbed (primarily by haying) native grassland, the habitat most like the native grassland grid, yielded five species: Sigmodon hispidus, Peromyscus
Table 3. Summary of numbers of different individuals of each rodent species caught in six habitats at Clymer Meadow, Hunt County, Texas, 1989-1992.

<table>
<thead>
<tr>
<th>Species</th>
<th>Undisturbed (grid)</th>
<th>Hayed native grassland</th>
<th>Bermuda-grass pasture</th>
<th>Undisturbed (grid)</th>
<th>Cedar elm-ash woodland</th>
<th>Wooded hilltops and mottes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sigmodon hispidus</td>
<td>153</td>
<td>94</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Peromyscus leucopus</td>
<td>7</td>
<td>23</td>
<td>5</td>
<td>52</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Peromyscus maniculatus</td>
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<td>15</td>
<td>4</td>
<td>46</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Neotoma floridana</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>20</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Reithrodontomys fulvescens</td>
<td>32</td>
<td>14</td>
<td>—</td>
<td>3</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Reithrodontomys humulis</td>
<td>7</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Mus musculus</td>
<td>—</td>
<td>3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Total rodents</td>
<td>206</td>
<td>149</td>
<td>12</td>
<td>119</td>
<td>3</td>
<td>4</td>
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<tr>
<td>Total traps set</td>
<td>1,800</td>
<td>1,344</td>
<td>150</td>
<td>1,080</td>
<td>90</td>
<td>69</td>
</tr>
<tr>
<td>Trapping efficiency</td>
<td>11.4%</td>
<td>11.1%</td>
<td>8.0%</td>
<td>11.1%</td>
<td>3.3%</td>
<td>5.8%</td>
</tr>
</tbody>
</table>

leucopus, Peromyscus maniculatus, Reithrodontomys fulvescens, and Mus musculus. Presence of Mus musculus and absence of Reithrodontomys humulis distinguished the disturbed grassland from the undisturbed grassland. A pasture dominated by coastal bermuda grass (Cynodon dactylon) and being lightly grazed by cattle during our trapping had a less-diverse rodent fauna (only Sigmodon hispidus, Peromyscus leucopus, and Peromyscus maniculatus) than native grassland. Trapping in wooded hilltop mottes produced a different set of three species (Sigmodon hispidus, Peromyscus leucopus and Neotoma floridana). The habitat with the most-depauperate rodent community was a low-lying woodland dominated by cedar elm and ash (Fraxinus); only Peromyscus leucopus was trapped there. Another factor possibly germane to differences in the rodent communities in these habitats is the presence or absence of imported fire ants. These ants were absent from the tract containing the two grid sites during the entire study, but were present in all hayed, grazed and other disturbed tracts.

Discussion

Habitat associations.—Sampling revealed the presence of six native species of ground-dwelling rodents (Sigmodon hispidus, Reithrodontomys fulvescens, Reithrodontomys humulis, Peromyscus leucopus, Peromyscus maniculatus, Neotoma floridana) and one exotic species (Mus musculus) in the various prairie habitats. The microhabitat selectivities of these species at Clymer Meadow generally corresponded with those reported for these species elsewhere in their ranges.
Though *Sigmodon hispidus* may be found in a variety of habitats, their greatest densities obtain in monocot-dominated situations where dense stands of grasses with a thick mulch layer and intermixed with forbs offer suitable cover (Kaufman & Fleharty 1974; Kincaid & Cameron 1985; McMurry et al. 1994). Cotton rats use less-favored habitats when population densities are high (Fleharty & Mares 1973); this tendency probably explains the isolated occurrence of a subadult cotton rat in the wooded draw of Clymer Meadow.

*Peromyscus leucopus* and *Peromyscus maniculatus* occurred in the grassland and wooded habitats at Clymer, with *Peromyscus leucopus* predominating in the woodland and achieving much lower densities in the grassland where there were similar densities of *Peromyscus maniculatus*. On Konza Prairie, white-footed mice achieved dramatically greater densities in wooded habitats than in habitats lacking trees (McMillan & Kaufman 1994), a trend also documented by Cummings & Vessey (1994). *Peromyscus maniculatus* in the tallgrass prairies of Kansas avoids sites with well-developed litter layers, selectively foraging instead in patches with sparse litter (≤1 cm high--Clark and Kaufman 1991). The low densities of deer mice in the Clymer grassland may be explained by the presence of thick, dense litter. Despite its widely documented preference for grassy areas (Kaufman & Fleharty 1974; Schmidly 1983; Schwartz et al. 1994), *Peromyscus maniculatus* also was caught frequently in the wooded draws of Clymer Meadow, where its greater-than-expected presence perhaps was related to microhabitat patchiness (McMillan & Kaufman 1994). This pattern probably was effected by the narrowness of the belts of woodland penetrating the more-extensive grasslands of the preserve.

In eastern Texas, *Reithrodontomys fulvescens* occurs in a variety of habitats, all of which include a significant component of grasses (Schmidly 1983). At Clymer Meadow, fulvous harvest mice were trapped only in undisturbed native grassland and in hayed native grassland, two situations in which little bluestem and switchgrass were the dominant grasses. Also caught in this undisturbed native grassland at Clymer Meadow was *R. humulis*, a species that appears to be uncommon in all eastern Texas localities from which it is known (Schmidly 1983; Wilkins 1991). There is evidence, however, that eastern harvest mice might be more abundant than most reports indicate (Dunaway 1968; Cawthorn & Rose (1989), using a modified trapping method that excluded larger species of rodents, estimated densities averaging about 20/ha, with peaks as high as 44.4/ha, in old fields in southeastern Virginia.
The habitats in which *Neotoma floridana* occurred at Clymer Meadow approximate those described for eastern woodrats in Kansas, where they preferred living in tangled underbrush in low-lying areas along timbered streams (Kellogg 1915). With the subsequent destruction of this habitat in Kansas, woodrats shifted to hedgerows where the dominant tree was osage orange (bois d’arc), and coralberry constituted a significant proportion of the understory (Rainey 1956). Wooded habitats, both in drainages and on hilltops, throughout the Clymer preserve boast numerous stick houses built by woodrats; preferred locations seem to be at the bases of multistemmed bois d’arc trees.

**Biogeographic considerations.**—Of the seven species of rodents sampled in the prairie habitats, one (*Reithrodontomys humulis*) was previously unknown from Hunt County; this westward extension of geographic range has been reported elsewhere (Wilkins 1991). Three additional native species of rodents, Taylor’s pygmy mouse (*Baiomys taylori*), hispid pocket mouse (*Chaetodipus [Perognathus] hispidus*), and thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), were anticipated but not found at Clymer preserve despite extensive sampling during an array of weather conditions during all seasons over 3 years. *Baiomys taylori*, a euryoecious species that frequently inhabits grassy areas, is known to the west in nearby Dallas and Denton counties (Schmidly 1983). Only in the 1960’s did this species enter north-central Texas as part of a continuing northward expansion from subtropical south Texas (Schmidly 1983; Pitts & Smolen 1989). Possibly, *Baiomys taylori* simply has not yet reached Clymer Meadow; regular monitoring might reveal its entry into the area in the next decade or two.

Having a well-documented statewide range (Davis & Schmidly 1994), *Chaetodipus hispidus* almost certainly is present at or in the vicinity of Clymer Meadow. My observations from work in eastern and central Texas are in agreement with McCarley’s (1959) report that *C. hispidus* is not abundant in habitats with clayey soils (e.g., blackland prairies), but is more common in habitats with well-drained, sandy soils (e.g., sandy alluvium along Brazos River in McLennan County, pers. obs.; Wilkins 1977; Wilkins & Schmidly 1980). Though Bailey’s distribution map (1905: plate XIII) for *S. tridecemlineatus* included the western half of Hunt County, no evidence of this species was found at Clymer Meadow. Continued sampling might yet reveal these species on this preserve.

The assemblage of ground-dwelling rodent species at Clymer preserve apparently is unique, different by at least one or two species from faunas
described in the few other studies of small-mammal demography in various habitats in eastern Texas. These studies include an inventory of mammalian species in the Big Thicket region (Schmidly et al. 1979, 1980); assessment of effects of mowing of highway rights-of-way vegetation on rodent species in Brazos and Madison counties (Wilkins 1977; Wilkins & Schmidly 1980); comparison of rodent communities on natural, reclaimed, and strip-mined habitats near Fairfield, Freestone County (Waggoner 1975); and studies of rodent population dynamics in coastal prairies near Houston (Joule & Cameron 1974; Cameron 1977; Cameron et al. 1979), and in old fields in the postoak savanna of Brazos County (Grant et al. 1985).

Little other work on the population dynamics of small mammals on native tallgrass Blackland Prairies in Texas has been conducted, and apparently none has been published. However, one such project was conducted in Falls County, north of Marlin, on the Dorothea Leonhardt Preserve, owned by the Nature Conservancy of Texas. The Leonhardt Prairie, a tallgrass prairie dominated by little bluestem and switchgrass, is located approximately 270 km SSW of Clymer Meadow. R. S. Baldridge and other faculty members and students of the Department of Biology, Baylor University (unpublished data), conducted mark-release-recapture studies of small mammals from 1984 until about 1987. They found *Sigmodon hispidus* and *Baiomys taylori* to be co-dominant species of the Leonhardt Prairie rodent community. Other ground-dwelling rodents at this site were *Peromyscus leucopus*, *Peromyscus maniculatus*, *Reithrodontomys fulvescens*, *Chaetodipus hispidus*, *Neotoma floridana*, and *Mus musculus*. Imported fire ants invaded the Leonhardt preserve near the end of the study.

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The efforts of many people contributed to the successful completion of this project. Jeff Weigel, of the Nature Conservancy of Texas, was involved significantly and enthusiastically in all administrative phases of the project. Numerous students from my classes at Baylor University provided much of the personpower needed in the field segments of the project; most notable among these were graduate students Russ Fraze and Rick Wiedenmann. W. Keith Hartberg, chairman of the Baylor Biology Department, facilitated this research by allowing use of departmental vehicles and other equipment. Prof. Walter Holmes, Baylor University, graciously identified several species of plants found on the preserve. Several Nature Conservancy interns, including Ben
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NOTES ON HARVEST MICE (*REITHRODONTOMYS*) OF THE BIG BEND REGION OF TEXAS

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Abstract.—Extensive live-trapping for small mammals on the Big Bend Ranch State Park, Texas, yielded several specimens of *Reithrodontomys fulvescens* and *Reithrodontomys megalotis* from a variety of habitat types. On two occasions, these two species of harvest mice were taken in sympatry. The ecological relationships and reproductive biology of these two species of harvest mice are reviewed. In addition, the distributions of *R. fulvescens*, *R. megalotis*, as well as their congener, *Reithrodontomys montanus*, in the Big Bend region of Texas are discussed.

The presence of three species of harvest mice (*Reithrodontomys fulvescens*, *R. megalotis* and *R. montanus*) in the Big Bend region of Texas has been previously documented (Schmidly 1977; Hall 1981; Jones & Jones 1992; Davis & Schmidly 1994). However, information is not available with regard to the details of geographic distributions and ecological relationships of these rodents in the area. In addition, little is known about the life histories of these species in the Trans-Pecos area of Texas (Schmidly 1977). This report is a summary of information obtained recently on the harvest mice of the Big Bend region of Trans-Pecos Texas.

Methods and Materials

Between January 1994 and April 1995, small mammals were sampled on the Big Bend Ranch State Park, Texas. This area was formerly known as the Big Bend Ranch State Natural Area. This area encompasses approximately 1087 square kilometers of Presidio and Brewster counties. Sherman live traps were set in the four major habitat types that exist in the area; Chihuahuan Desert scrub, Chihuahuan Desert grassland, juniper roughland, and riparian woodland. During the course of this study, 7,439 traps were set. Traplines consisted of 40-50 traps baited with rolled oats, and set at 10 meter intervals. They were set approximately one hour before sundown and retrieved approximately one hour after sunrise the following morning. Animals acquired were identified and voucher specimens (standard museum skin and skull) were prepared. From selected specimens, tissues (muscle, liver, heart, and kidney) were collected and immediately frozen in liquid nitrogen.
In the following accounts, all measurements provided are in millimeters. All localities are based on Universe Transverse Mercator (UTM) coordinates taken from a hand held global positioning system. As a reference point for these UTM coordinates, Big Bend Ranch State Park Headquarters (Sauceda Ranch), which has UTM coordinates 13601203E, 3260197N, is situated approximately 9 km S, 41 km E of Presidio. Voucher materials (TTU numbers) and frozen tissues (TK numbers) are deposited in the Collection of Recent Mammals in the Natural Science Research Laboratory of the Museum of Texas Tech University.

Results and Discussion

*Reithrodontomys fulvescens* (fulvous harvest mouse).—Although this species has an extensive geographic range in North and Central America (Hall 1981; Spencer & Cameron 1982), it occurs mostly east of the 100th meridian in Texas, except for parts of the Panhandle and the Trans-Pecos region (Schmidly 1977; Jones & Jones 1992; Davis & Schmidly 1994). This species was recorded previously from single localities in Presidio and Reeves counties, from four localities in Brewster County, and from five localities in Jeff Davis County, Texas (Schmidly 1977). During this study, seven specimens of *R. fulvescens* were obtained from three locations in Presidio County, and a single specimen from one site in western Brewster County, all within the boundaries of the Big Bend Ranch State Park.

According to Schmidly (1977), in the Trans-Pecos, *R. fulvescens* favors rough grasslands. However, all seven individuals acquired from Presidio County during this study were taken in riparian habitat. Each was captured along small, permanent streams where cottonwood (*Populus* sp.), willow (*Salix* sp.), false willow (*Baccharis* sp.), and various grasses were the dominant plant species. Interestingly, *R. megalotis* was taken along with *R. fulvescens* at two of the three localities in Presidio County. Such close ecological associations of these two species of harvest mice were not reported previously for the Big Bend region of West Texas (Schmidly 1977), Chihuahua, Mexico (Anderson 1972), or Coahuila, Mexico (Baker 1956). Other rodents associated with these riparian areas included the white-footed mouse (*Peromyscus leucopus*), the deer mouse (*P. maniculatus*), the white-ankled mouse (*P. pectoralis*), and the hispid cotton rat (*Sigmodon hispidus*).
The single specimen of *R. fulvescens* taken from western Brewster County was captured in a dry, shallow arroyo in the basin of the unique geological formation known as the Solitario. The habitat at this site was Chihuahuan Desert scrub dominated by mesquite (*Prosopis* sp.), catclaw (*Acacia* sp.), and medium grass. Other small mammals taken in conjunction with this specimen included Nelson’s pocket mouse (*Chaetodipus nelsoni*), the desert pocket mouse (*C. penicillatus*), and Merriam’s kangaroo rat (*Dipodomys merriami*).

In Texas in general, fulvous harvest mice are known to breed from February to October (Davis & Schmidly 1994). However, a male in reproductive condition (testes 10 by 5 mm) was captured on 10 November, and a gravid female (3 embryos with crown-rump length of 14 mm) was taken on 17 November. Given a gestation period of about 21 days (Davis & Schmidly 1994), these data suggest that the breeding season in the Big Bend region may extend well into November. Non-gravid females were obtained on 10 January and 13 and 14 February. In addition, three non-reproductively active males (testes 4 by 2 mm) were taken on 13 February.

**Material examined.**—Brewster County: Big Bend Ranch State Park, UTM coordinates 13 617281E, 3261484N, one specimen (TTU 67413). Presidio County: Big Bend Ranch State Park, UTM coordinates 13 587250E 3262918N, five specimens (TTU 67407, TK 41751; TTU 67408-67410; TTU 67414, TK 46437); Big Bend Ranch State Park, UTM coordinates 13 601619E 3260741N, one specimen (TTU 67411); Big Bend Ranch State Park, UTM coordinates 13 586937E 3262923N, one specimen (TTU 67412).

*Reithrodontomys megalotis* (western harvest mouse).—This species has a large geographic range in North America (Hall 1981; Webster & Jones 1982), but in Texas is known only from the western Panhandle, the northwestern Edwards Plateau, and the Trans-Pecos region (Schmidly 1977; Jones & Jones 1992; Davis & Schmidly 1994; Goetze et al. 1995). This mouse was considered uncommon in Coahuila, Mexico (Baker 1956), but was reported as widespread both geographically and ecologically in Chihuahua, Mexico (Anderson 1972). According to Schmidly (1977), "This is the most widely distributed harvest mouse in the Trans-Pecos..." In addition to four localities reported previously from Presidio County (Schmidly 1977), 10 specimens of the western harvest mouse were collected during this study from seven localities within Big Bend Ranch State Park, Presidio County.
In the Trans-Pecos, *R. megalotis* is reported to prefer grasslands with dense ground cover (Schmidly 1977). However, of the seven sites from which collections of this mouse were made, only two fit this description. At one of these sites, two western harvest mice were taken in tall grass associated with yucca (*Yucca* sp.) and mesquite. Other mammals taken from this site included the deer mouse and Mearn’s grasshopper mouse (*Onychomys arenicola*). At the other grassland site, a single *R. megalotis* was taken in heavily grazed short grass with thick desert-willow (*Chilopsis* sp.). Associated small mammals included the deer mouse and the white-footed mouse.

As mentioned previously, western harvest mice also were found at two riparian localities. See the above account on *R. fulvescens* for specifics.

The three remaining sites from which specimens of western harvest mice were acquired are best described as desert scrub. Associated vegetation included creosotebush (*Larrea* sp.), mesquite, mariola (*Parthenium* sp.), catclaw, and various grasses. The desert pocket mouse, Merriam’s kangaroo rat, the cactus mouse (*Peromyscus eremicus*), the deer mouse, and the southern plains woodrat (*Neotoma micropus*) also were taken at these localities.

Western harvest mice are considered to breed throughout the year (Schmidly 1977). Reproductive data regarding specimens from this study are as follows. A male collected in January had testes measuring 5 by 1 mm. Specimens obtained in February included five males with testes measuring 3 by 2 mm (two specimens), 6 by 4 mm, 5 by 3 mm, and 2 by 2 mm, as well as two non-gravid females. A female bearing three embryos (crown-rump length 8 mm) was taken in April. One non-gravid female was collected in November.

**Material examined.**—Presidio County: Big Bend Ranch State Park, UTM coordinates 13 600694E, 3259751N, one specimen (TTU 67415); Big Bend Ranch State Park, UTM coordinates 13 587250E, 3262918N, two specimens (TTU 67416-67417, TK 41752); Big Bend Ranch State Park, UTM coordinates 13 601619E, 3260741N, two specimens (TTU 67418-67419); Big Bend Ranch State Park, UTM coordinates 13 576836E, 3296251N, one specimen (TTU 67420, TK 41778); Big Bend Ranch State Park, UTM coordinates 13 576970E, 3296222N, one specimen (TTU 67421); Big Bend Ranch State Park, UTM coordinates 13 601973E, 3253265N, one specimen (TTU 67605, TK 46450); Big Bend Ranch State Park, UTM coordinates 13 605746E, 3261330N, two specimens (TTU 67606, TK 46458; TTU 67607, TK 46460).
Reithrodontomys montanus (plains harvest mouse).—This species is distributed widely in central and southwestern North America (Hall 1981; Wilkins 1986), and it ranges throughout much of Texas (Jones & Jones 1992; Davis & Schmidlly 1994). However, Schmidlly (1977) considered it to be the rarest of the species of Reithrodontomys occurring in the Trans-Pecos region. Other than the records of R. montanus summarized by Jones et al. (1993), no recent information is known on this species from the Big Bend region of Texas. Reithrodontomys montanus was reported from five localities in Chihuahua, Mexico, the southern limit of the geographic range of the species (Anderson 1972).

The three species of harvest mice (R. fulvescens, R. megalotis and R. montanus) in the Big Bend Region of Texas should be subjected to thorough review with regard to systematic affinities. In addition, given the overlaps of the geographic ranges of R. fulvescens and R. megalotis in restricted habitats on the Big Bend Ranch State Park, it would appear that unique opportunities exist there for detailed studies of the ecological relationships of these two sympatric species.

Acknowledgments

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KARYOTYPES OF SEVEN SPECIES OF NORTH AMERICAN WRENS (PASSERIFORMES: TROGLODYTIDAE)

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Abstract.—Karyotypes, new to cytology, are described for seven North American species of wrens (Troglodytidae); Campylorhynchus brunneicapillus (2n = 74), Salpinctes obsoletus (2N = 80), Catherpes mexicanus (2N = 80), Thryothorus ludovicianus (2n = 76), Thryomanes bewickii (2n = 76), Cistothorus platensis (2N = 76), and Cistothorus palustris (2N = 76). All species examined share the first three macrochromosomes.

Compared to other vertebrate classes (e.g. mammals and reptiles), avian karyology is poorly known. Less than 10% of the world’s species of birds have been karyotyped, of which very few have been passerines (Takagi & Sasak 1974; Tegelstrom & Ryttman 1981; Shields 1983; 1985; De Boer 1984). The family Troglodytidae includes some 45 species in 15 different genera (Morony et al. 1975; Sibley & Monroe 1990). Of these, only two species have been karyotyped. Udagawa (1956) described the chromosomes of the Nearctic species, Troglodytes troglodytes (2n = 86) and De Lucca & Chamma (1977) reported those of the neotropical wren, Thryothorus leucotis (2n = 78).

Nine species of wrens occur in North America north of Mexico (AOU 1983). This study provides the first description of the chromosomes of seven of these species: Cactus Wren (Campylorhynchus brunneicapillus), Rock Wren (Salpinctes obsoletus), Canyon Wren (Catherpes mexicanus), Carolina Wren (Thryothorus ludovicianus), Bewick’s Wren (Thryomanes bewickii), Sedge Wren (Cistothorus platensis), and Marsh Wren (Cistothorus palustris). Nomenclature follows that of the AOU Check-list of North American Birds (1983). This study represents the only cytogenetic information reported for these species.

Materials and Methods

Cytological techniques followed those of Christidis (1985) and Hafner & Sandquist (1989). A chromosome was designated as a macrochromosome if either the centromere or separate arms could be differentiated.
All other chromosomes were designated as microchromosomes. At least 10 metaphase cells of each species were examined in order to determine the diploid number. Both sexes were examined for each species. A total of 26 specimens were examined during the course of this study. Specimens were collected in accordance with scientific collecting permit numbers PRT-674149 (U.S. Fish and Wildlife Service) and SPR-0290-021 (Texas Parks and Wildlife Department) issued to Terry C. Maxwell. Voucher study skins of 24 salvageable specimens are deposited with the holdings of the Angelo State Natural History Collections (ASNHC) at Angelo State University.

Material examined.—Thryomanes bewickii.—5.5 mi N, 4.5 mi W of San Angelo, Tom Green County, Texas, one male specimen (ASNHC 1058) and two female specimens (ASNHC 1054, 1056); 5 mi S of Christoval, Tom Green County, Texas, one male specimen (ASNHC 1057). Thryothorus ludovicianus.—5 mi S of Christoval, Tom Green County, Texas, two male specimens (ASNHC 1050, 1051) and one female specimen (ASNHC 1053); 4 mi S of Christoval, Tom Green County, Texas, one male specimen (ASNHC 1048). Campylorhynchus brunneicapillus.—10 mi S 4.5 mi W of San Angelo, Tom Green County, Texas, one male specimen (ASNHC 1073); 10 mi SW of San Angelo, Tom Green County, Texas, one male specimen (ASNHC 694); 6.3 mi N, 13.2 mi W of Mertzon, Irion County, Texas, one female specimen (ASNHC 1074). Salpinctes obsoletus.—10.5 mi S, 2.3 mi W of San Angelo, Tom Green County, Texas, three female specimens (ASNHC 1061, 1062, 1063). Catherpes mexicanus.—6.3 mi N, 13.2 mi W of Mertzon, Irion County, Texas, one female specimen (ASNHC 1063); 2 mi. S, 1 mi W of Leakey, Real County, Texas, one male specimen (ASNHC 1065) and one female specimen (ASNHC 1064). Cistothorus platensis.—11.8 mi N of Freeport, Brazoria County, Texas, two male specimens (ASNHC 1066, 1067) and three female specimens (ASNHC 1068, 1069 1070). Cistothorus palustris.—4 mi S of San Angelo, Tom Green County, Texas, one male specimen (ASNHC 1072) and one female specimen (ASNHC 1071).

Results and Discussion

The diploid number of chromosomes of wren species examined during this study ranges from 74 in Campylorhynchus to 80 in both Salpinctes and Catherpes and is similar to diploid numbers reported in most birds. Shields (1980) reported that 70% of all birds karyotyped have diploid numbers between 76 and 84. Although no intraspecific polymorphisms were detected in karyotypes examined during this study, larger sample
Figure 1. Karyotype of *Campylorhynchus brunneicapillus* (ASNHC 694 δ). Scale is 10 μm.

Figure 2. Karyotype of *Salpinctes obsoletus* (ASNHC 1061 ♂). Scale is 10 μm.

sizes with wider geographic representation would be required to accurately assess intraspecific variation.

*Campylorhynchus brunneicapillus* (Cactus Wren) exhibits a diploid number of 74 (Fig. 1). The eight largest pairs of macrochromosomes (including the sex chromosomes) are distinguishable by size from the remaining 29 pairs of smaller microchromosomes. The two largest pairs of macrochromosomes are submetacentric, the third largest pair is subtelocentric, the next two pairs are submetacentric and the sixth and seventh pair are telocentric. The eighth pair of macrochromosomes are the sex chromosomes. In this species, the W chromosome is telocentric,
whereas the Z chromosomes are subtelocentric.

*Cistothorus palustris* (Marsh Wren) (Fig. 2) and *C. platensis* (Sedge Wren) (Fig. 3) appear to have identical karyotypes, each with a diploid number of 76. They have eight pairs of macrochromosomes (including the sex chromosomes) and 30 pairs of microchromosomes. In both species, the largest pair is submetacentric, the next four pairs are subtelocentric, and the two smallest pairs are telocentric. The W chromosome appears to be telocentric, whereas the Z chromosome is subtelocentric.

*Thryomanes bewickii* (Bewick’s Wren) (Fig. 4) and *Thryothorus ludovicianus* (Carolina Wren) (Fig. 5) also appear to exhibit identical karyotypes with a 2n of 76. They have nine pairs of macrochromosomes (including the sex chromosomes) and 29 pairs of microchromosomes. All other species in this study exhibited eight pairs of macrochromosomes. The largest pair for both species are submetacentric, the next two pairs are subtelocentric, the fourth pair is submetacentric and the four smallest pairs are telocentric. Again, the W chromosome is telocentric, whereas the Z chromosomes are subtelocentric. The diploid number of 76 observed in this study for *T. ludovicianus* differs from that reported for the only other karyotyped
species within the genus. De Lucca & Chamma (1977) reported a 2n of 78 for *T. leucotis*.

*Salpinctes obsoletus* (Rock Wren) (Fig. 6) and *Catherpes mexicanus* (Canyon Wren) (Fig. 7) have very similar karyotypes, both with a diploid number of 80. Both have eight pairs of macrochromosomes (including the sex chromosomes) and 32 pairs of microchromosomes. In both species, the largest pair is submetacentric, the next four pairs are subtelocentric, and the two smallest pairs are telocentric. The Z chromosome appears to be a large telocentric. The only difference in
the karyotypes appears to be the W chromosome. In the Rock Wren, the W chromosome is metacentric, whereas that of the Canyon Wren appears to be telocentric. Some authors have considered these two species to be congeneric (Mayr & Short 1970; Morony et al. 1975).
All genera of wrens that have been karyotyped share the first three largest pairs of macrochromosomes, with one exception; the second pair in *Campylorhynchus* is submetacentric instead of subtelocentric as in all the others. The tendency for the largest three or four pairs of chromosomes to be identical among different groups of birds is fairly common (Stock et al. 1974; Ryttman et al. 1979; Ryttman & Tegelstrom 1981). *Cistothorus, Catherpes,* and *Salpinctes* all share pairs four and five whereas *Thryothorus, Thryomanes,* and *Campylorhynchus* share pair four. With regard to pair five, *Campylorhynchus* is submetacentric, whereas *Thryothorus* and *Thryomanes* are both telocentric. All species share pairs six and seven. Only *Thryothorus* and *Thryomanes* have the eighth pair of macrochromosomes. *Thryomanes, Thryothorus, Cistothorus,* and *Campylorhynchus* all appear to share the Z and W chromosomes. *Catherpes,* and *Salpinctes* share the same Z chromosome but appear to have different W chromosomes.

This study represents the only cytogenetic information reported for these species of wrens. Further karyological investigation, with chromosomal banding, should provide clarification of divisions within this phylogenetically challenging assemblage.

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CHANGES IN THE GEOGRAPHIC CENTERS OF THE POPULATION OF TEXAS FROM 1850 TO 1990

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Abstract.—This study presents a spatial and tabular analysis of the movement of the center of population of Texas for each of the Decennial Censuses from 1850 to 1990. The population center’s geographic location has remained remarkably constant over the past 140 years, demonstrating that even with dramatic spurts of population growth at various times and in various locations throughout the state, the relative distribution of Texas’s city sizes by population has remained surprisingly constant. This suggests a regularity and stability in the Texas settlement pattern over time.

Officials of the US Bureau of the Census state that a nation or state’s gravity center of population is the “preeminent measure for analyzing population distribution and change” (US Bureau of the Census 1974). Perturbations in the location of such a center reflects ongoing economic and settlement changes. This study presents a spatial and tabular analysis of the movement of the center of population of Texas for each of the Decennial Censuses from 1850 to 1990.

One could envision the center of the population of Texas as the demographic heart or balance point of the state’s population distribution. On an imaginary, flat, weightless and rigid map of Texas, where each Texan is assumed to have equal weight, and where each Texan exerts an influence on the center of population proportional to his or her distance from the center, the state is demographically balanced at this population center of gravity. Viewed another way, if the state’s total population aspired to be spatially efficient by assembling at a point whose location minimized the aggregate sum of all straight-line travel distances from their residences to this point, then this pivotal point or group centroid would represent the state’s population center or demographic heart.

The present population settlement pattern of Texas can be characterized as clusters of densely populated metropolitan areas, their inter-metropolitan peripheries, and thinly populated rural sectors (Davies 1986:Figure 1). The coalescence of Dallas-Fort Worth, Waco, Austin, San Antonio and the Houston-Bay area into a triangle of dense, conjoining urban corridors, is a regional feature that contrasts with the state’s more isolated cities, such as Amarillo, Lubbock, McAllen, Brownsville, El Paso and Wichita Falls.
Center Computation

In calculating the location of the center of population of Texas for the 15 censuses between 1850 and 1990, along with its movement from decade to decade, the county was used as the geographic unit of measurement. The coordinates of a county's center of population must be calculated for the state's 254 counties, for each of the 15 censuses from 1850 to 1990.

A county's population center generally lies around its most populous city. If a county's population does not coalesce in this manner, a center is determined that reflects the proportional influences on its location of the county's three or four largest cities. A typical population pattern found in most Texas counties is a dispersion around a radial transportation network centered on a county seat, with smaller settlements strung out along the highway, and scattered populations filling the interstices.

The population center of each county north and south of the parallel line is multiplied by the distance of this center from the parallel to provide the north and south moments for that county. The county's east and west moments from the meridian line are similarly derived. In calculating the moments the distances are measured in minutes of arc. These moments are the directional corrections each county population exerts on the location of the state's center of population. Under a weighted-mean system these exertions are expressed in a way that standardizes correctional differences.

The county center of population moves north or south, or east or west of the parallel and meridian lines respectively, depending upon which directional product (population times distance) or moment is in excess. The difference between the north and south product sum or moments is divided by the total population of the county to give the number of degrees, minutes, or seconds of arc that the county's center of population is north or south of this parallel line. Similarly, the difference between the east and the west product sums is divided by the total county population to give the measure of arc the population center is east or west of the meridian line. For example, the center of population of Anderson County in 1850 is calculated to lie near Palestine, at 95°38' West longitude, and 31°46' North latitude.

To calculate the center of population of Texas, an assumption is first made as to its location in 1850. From archival records on the distribution of 212,592 people in 1850 in Texas, the state's population center
is assumed to intersect at a meridian of longitude, 97°West, and a parallel of latitude, 31°North, in northern Milam County. One can perceive of this meridian line and parallel line as the axes of moments crossing the state.

The relationship of the coordinates of each of the 254 county centers of population to the coordinates of the center of population of Texas for each of the 15 Decennial Censuses is now estimated. For example, the relationship or location of Anderson County’s center of population (95°38’ West, 31°46’ North) to that of the population center of Texas located in Milam County in 1850 (97°West, 31°North) is recorded as 82 min East, and 46 min North of this Milam County location. This difference is Anderson County’s distance or correctional factor.

The populations of the 254 counties for each of the individual 15 Decennial Censuses are then multiplied by their own correctional distances to provide the population influence each county has on the center of population of Texas for that census date. For example, in 1850 Anderson County’s population was 2,884. Therefore, in 1850 Anderson County’s population exerted an influence, or a refinement on the coordinates of the population center of Texas of 236,488 people-min East (82 min East x 2,884 people), and 132,664 people-min North (46 min North x 2,884 people).

The sum of all 254 county population influences is the total influence or pull of all county populations on the state’s center of population for each census between 1850 and 1990. The total westward influence is subtracted from the total eastward influence, and the total southern influence is subtracted from the total northern influence. In 1850, this statewide population influence on the center of population of Texas is 15,495,632 people-min to the East, and 673,006 people-min to the North.

These above East and North correctional influences are then divided by the 1850 population of Texas of 212,592 to give a correctional factor in longitude and latitude to the 1850 population center of Texas of 72.8891 people-min to the East (15,495,632/212,592), and 3.165 people-min to the North (673,006/212,592). This is the total moment-arm correction on the center of population of Texas for the 1850 census date. The assumed center of population of Texas for 1850 of 97°West, and 31°North, is now adjusted by this statewide correctional factor of 72.8891 min East, and 3.1657 min North, to establish the final location of the center of population of Texas of 95°47'
Table 1. Geographical position of Texas' centers of population from 1850 through 1990, followed by the resident county of each site and the directional movement in miles since the last census.

<table>
<thead>
<tr>
<th>Year</th>
<th>Longitude</th>
<th>Latitude</th>
<th>County (*)</th>
<th>Directional Movement (in miles)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1850</td>
<td>95°47'7&quot;</td>
<td>31°3'10&quot;</td>
<td>Madison (Midway)</td>
<td></td>
</tr>
<tr>
<td>1860</td>
<td>96°14'32&quot;</td>
<td>31°13'25&quot;</td>
<td>Leon (Marquez)</td>
<td>23.5  10.2</td>
</tr>
<tr>
<td>1870</td>
<td>96°21'55&quot;</td>
<td>31°9'11&quot;</td>
<td>Robertson (Easterly)</td>
<td>6.3   4.2</td>
</tr>
<tr>
<td>1880</td>
<td>96°39'27&quot;</td>
<td>31°22'48&quot;</td>
<td>Limestone (Thornton)</td>
<td>15.0  13.6</td>
</tr>
<tr>
<td>1890</td>
<td>96°51'56&quot;</td>
<td>31°28'28&quot;</td>
<td>Falls (Perry)</td>
<td>10.2  5.7</td>
</tr>
<tr>
<td>1900</td>
<td>96°54'12&quot;</td>
<td>31°28'41&quot;</td>
<td>McLennan (Riesel)</td>
<td>1.9   0.2</td>
</tr>
<tr>
<td>1910</td>
<td>97°15'19&quot;</td>
<td>31°31'46&quot;</td>
<td>McLennan (Waco)</td>
<td>18.0  3.1</td>
</tr>
<tr>
<td>1920</td>
<td>97°19'33&quot;</td>
<td>31°29'26&quot;</td>
<td>McLennan (McGregor)</td>
<td>3.6   2.3</td>
</tr>
<tr>
<td>1930</td>
<td>97°34'9&quot;</td>
<td>31°22'41&quot;</td>
<td>Coryell (Oglesby)</td>
<td>12.4  6.7</td>
</tr>
<tr>
<td>1940</td>
<td>97°28'15&quot;</td>
<td>31°15'32&quot;</td>
<td>Bell (Pendleton)</td>
<td>5.0   7.1</td>
</tr>
<tr>
<td>1950</td>
<td>97°35'59&quot;</td>
<td>31°7'46&quot;</td>
<td>Bell (Nolanville)</td>
<td>6.6   7.8</td>
</tr>
<tr>
<td>1960</td>
<td>97°41'48&quot;</td>
<td>31°5'47&quot;</td>
<td>Bell (Killeen)</td>
<td>5.0   2.0</td>
</tr>
<tr>
<td>1970</td>
<td>97°32'12&quot;</td>
<td>31°5'0&quot;</td>
<td>Bell (Nolanville)</td>
<td>8.2   0.8</td>
</tr>
<tr>
<td>1980</td>
<td>97°28'1&quot;</td>
<td>30°59'24&quot;</td>
<td>Bell (Salado)</td>
<td>3.6   5.6</td>
</tr>
<tr>
<td>1990</td>
<td>97°26'54&quot;</td>
<td>30°58'28&quot;</td>
<td>Bell (Little River)</td>
<td>1.0   0.9</td>
</tr>
</tbody>
</table>

(*) Nearest town to the geographic center within the county.

West, and 31°3' North for 1850. This procedure is repeated to establish the coordinates of the center of population of Texas for the 7th through the 21st United States Censuses, 1850-1990 (Table 1, Figure 1).

Center Movement

The location and movement of the state's center of population reflects the direction the population of Texas has grown and, to a certain extent, the direction the economic life of the state has taken. What Texans do for a living has a profound effect on the growth and shape of the state's urban pattern and the shifts in the fortunes of its various regions.

As to directional movement what has been the directional movement of this center over this 140 year interlude, and how extensive has this movement been? Are there regularities, cycles, and underlying mechanisms associated with its location over this 140 period? Figure 1 shows that from 1850 to 1910 Texas's center of population moved due west. Then from 1910 to 1990 it veered almost directly south, with a slight easterly gait. The decided southward direction shows the pulling
effect or influence on the center’s location of large population gains in Houston, Austin, San Antonio and the Gulf city complex. This southward drift would be even more emphatic if it were not counter-balanced by the population growth of the Dallas-Fort Worth-Denton metropolitan area.

Although Texas has the greatest area of any of the continental 48 states, the movement of its center of population is not large, since “the population development in nearly all parts of the state has been nearly uniform” (US Bureau of Census 1974). The accumulated straight-line movement of the center for this 140 year period is a mere 145 miles, or a shift of 10.3 miles every 10 years. The center has shown little movement over the last 40 years being firmly ensconced in Bell County. Table 1 shows in straight-line distances the direction West, East, North or South this population center dislocated for every census decade. For example, the population center traveled 18 miles West, and 3.1 miles North, between 1900 and 1910. The center’s shortest movements occur from 1970 to 1980, and from 1980 to 1990, when Texas gained its largest ever absolute population increases, some 3.03 million people, and 2.76 million people, respectively. This reemphasizes the almost uniform constancy of this absorption of people into the settlement pattern of Texas.
In comparison with the movement and the direction of the center of population of the nation and the remaining states, what has been the fate of the center of Texas? The US Bureau of the Census has calculated the center of population for the United States since the first census of 1790. Then the U.S. center of population was located in Maryland, some 23 miles east of Baltimore. By 1990 this population center had migrated southwestward to a site in southern Missouri as a reflection of the influence of the nation’s population growth in the west and the south. At intermittent times since 1880, the Bureau has also calculated the center of population for each state, principally, from 1880 to 1920, and from 1950 to 1970. Using the last period some 8, 17, 7, and 9 states exhibit North, South, East or West movements respectively, with 9 states and the District of Columbia showing no directional trend. For 1950 to 1970 Texas joins the 17 states with a southern drift and is also similar to 16 other states in that its center of population lies close to its state capital. Nevada’s center of population exhibits the greatest motion with 41.2 miles, and 32.2 miles, for 1950 to 1960, and 1960 to 1970 respectively. Rhode Island had the smallest movement of 0.5 mile and 0.3 miles, with the center of population of Texas moving five miles and six miles for these same periods.

Sources of Error/Comparisons

Some potential sources of error in the authors calculation of the center relate to the accuracy of the US Bureau of the Census’s county population counts, the assumption that the grid of longitudes and latitudes over Texas is perfectly flat, when the surface is very slightly curved, and the authors use of the county as the geographic unit of analysis.

This study and the US Bureau of the Census used different geographical units in the calculation of the population center of Texas for the decades when such comparisons were permissible. The geographic unit used by the Bureau groups the population of Texas by square degrees (that is, by areas included between consecutive parallels and meridians). This study used the county as the geographical unit of analysis. Differences in the siting of the center of population of Texas is almost negligible when either geographic unit of analysis is used (Table 2). This suggests that the county is as effective a geographic unit of analysis as that of square degrees. Furthermore, the county population is more easily obtainable and understandable as a unit of analysis than that of square degrees.
Table 2. Comparison of the geographical centers of Texas as determined by the U.S. Bureau of Census versus this study followed by the differences in miles between the two studies. The U.S. Census Bureau did not calculate the geographical center of Texas for 1930, 1940, 1980 or 1990.

<table>
<thead>
<tr>
<th>Year</th>
<th>U.S. Bureau Census Longitude</th>
<th>U.S. Bureau Census Latitude</th>
<th>This Study Longitude</th>
<th>This Study Latitude</th>
<th>Difference in Miles</th>
</tr>
</thead>
<tbody>
<tr>
<td>1880</td>
<td>96°38'30&quot;</td>
<td>31°20'50&quot;</td>
<td>96°39'27&quot;</td>
<td>31°22'48&quot;</td>
<td>2.1</td>
</tr>
<tr>
<td>1890</td>
<td>96°50'52&quot;</td>
<td>31°26'11&quot;</td>
<td>96°51'56&quot;</td>
<td>31°28'28&quot;</td>
<td>2.5</td>
</tr>
<tr>
<td>1900</td>
<td>96°52'56&quot;</td>
<td>31°28'35&quot;</td>
<td>96°54'12&quot;</td>
<td>31°28'41&quot;</td>
<td>1.5</td>
</tr>
<tr>
<td>1910</td>
<td>97°15'14&quot;</td>
<td>31°31'23&quot;</td>
<td>97°15'19&quot;</td>
<td>31°31'46&quot;</td>
<td>0.4</td>
</tr>
<tr>
<td>1920</td>
<td>97°19'12&quot;</td>
<td>31°28'34&quot;</td>
<td>97°19'33&quot;</td>
<td>31°29'26&quot;</td>
<td>0.9</td>
</tr>
<tr>
<td>1950</td>
<td>97°35'10&quot;</td>
<td>31° 7'30&quot;</td>
<td>97°35'59&quot;</td>
<td>31° 7'46&quot;</td>
<td>0.8</td>
</tr>
<tr>
<td>1960</td>
<td>97°40'59&quot;</td>
<td>31° 5'56&quot;</td>
<td>97°41'48&quot;</td>
<td>31° 5'47&quot;</td>
<td>0.7</td>
</tr>
<tr>
<td>1970</td>
<td>97°31'30&quot;</td>
<td>31° 4'52&quot;</td>
<td>97°32'12&quot;</td>
<td>31° 5' 0&quot;</td>
<td>0.6</td>
</tr>
</tbody>
</table>

Results and Discussion

In 1850 when Texas’s population totaled 212,529, the state’s population center was located at longitude 95°47'7", and latitude 31°3'10", around the town of Midway in Madison County, (sited in Walker County in 1850). One hundred and forty years later, with Texas’s population registering 17 million in 1990, the state’s population center had shifted to longitude 97°26'54", and latitude 30°58'28", near the town of Little River in Bell County. The directional movement of the center of population of Texas has moved West and then from 1910 to the present, almost vertically South (Figure 1). In the course of this 140 year interlude, the population center had transported little more than 145 miles, a rate of a mere mile a year.

Why is the overall location of the center of population of Texas so constant over these 140 years, when various parts of the state have experienced dissimilar spurts of growth at different times, which translates into increases in settlement size where that growth occurs? The maturation of the Texas urban system has resulted from spatial instabilities in which random discoveries of the state’s residue of available energy that evoked the rise of such cities as Amarillo or Odessa, became amplified, triggered growth, and in the process remolded the state’s settlement structure. As Texas went through a series of growth cycles, different parts of its present urban system emerged.

Distinct differences in the pace of urbanization occurred for different regions of Texas during the period 1890-1980. For expediency, the state has been divided into six broad regions, within whose arbitrary
boundaries estimates were made of the proportional increase in the pace of urbanization for 1890 to 1980 (Davies 1986: Figure 9). Generally, it is assumed that the Panhandle and West Texas (PWT) is the rural bastion of Texas. Yet from 1890 onward, following an attack on the state’s oil and gas resources, it underwent a proportional increase in the rate of urbanization far in excess of other Texas regions. This is obviously not true for absolute numerical increases, since the Dallas and North Texas Region (DNT), the Central Texas Region (CT), and the Houston and Gulf Coast Region (HGC) started off with much larger initial population bases.

What is much more significant than the mere numerical increase in the urban population of each region is the proportional rate of growth experienced by these diverse areas. The East Texas region experienced the slowest rate of urban growth. The other regional profiles are similar, with the Houston Gulf Coast Region the front runner, although lagging well behind the PWT region in the proportional rate of growth. The logarithmic curves show almost parallel slopes since 1960 for all regions, suggesting that the pace or rate of urbanization in Texas is now fairly uniform throughout the state (Davies 1986).

While pressure exerted by each individual Texan on the state’s population center increases in proportion to the distance traveled away from it, making population growth in such peripheral cities as Tyler-Longview-Marshall, Midland-Odessa, Laredo-El Paso and so forth, a more powerful relative influence on the center’s location than similar population growth in cities close to the center, such as those found in the state’s urban triangle (Dallas-Fort Worth, Austin, San Antonio and Houston) the larger population increases in this triangle, counters or nullifies the stronger relative influence of population growth in cities more distant from the center. The circular and cumulative causation behind the population growth of Texas since its founding as a state creates a multiplier effect, in that the regional dominance of the state’s heartland or triangle has hardly weakened over this 140 year interlude.

Whatever population increase has occurred in the state’s peripheral locations over the past 140 years, such increases failed to substantially affect the location of the state’s population center. In fact the influence is almost negligible when the locations of the center in Figure 1 is examined. This affirms the fact that for the past 140 years, the pace or rate of population absorption into the settlement pattern of Texas has been fairly uniform throughout the state. The present population of Texas has grown, as Malthus observed, exponentially, that is by
constant proportions and has been absorbed into the state’s settlement pattern according to the law of the urban hierarchy of Texas, which is the law of regularity (Davies 1986).

The constancy of the center’s location demonstrates that even with these spurts of population growth at various times and in various locations, the distribution of the city sizes of Texas by population, relative to each other, has remained remarkably constant, suggesting a regularity and stability in the Texas settlement pattern over time. If Texas cities are ranked in size from the largest downward, then the population of a given city tends to be equal to the population of the largest city divided by the rank of the given city. The J-shaped curve of Figure 10 of Davies (1986) (which is a plot of the city sizes of Texas and rank for selected years from 1860 to 1980) suggests that, as the overall population of Texas increased, Texas cities remained distributed in simple rank conformance.

The straightening of population curves (Davies 1986: Figure 10) over time for Texas is evidence of increasing regularity (like that of the United States as a whole) and suggests that in the development of the urban system of Texas two conditions prevail: equal increases in the number of towns of the lower size order and uniform distribution of the population increment through most city sizes. The rank-size distribution of Texas is a logical outcome or a by-product of its urban system and is sufficiently stable to allow one to project future patterns.

It appears that whatever the general growth of the Texas economy, this growth is distributed throughout the urban system, so that no one city class size monopolizes all the growth at any one time. It also appears that in the history of the urban development of Texas, a city begins with a random size and thereafter grows in an exponential manner, that is, proportional to its size. The Texas urban hierarchy grows under the law of allometric growth which is to say that the rate of growth of an individual city within the system is proportional to that of the system as a whole. The whole process of the civilization of Texas has been largely one of the aggregation of greater and greater numbers of people into limited areas; an apparently irresistible pressure to work toward a climax state, a provisionally stable pattern.

In a spatial context, since distance is an inconvenience one should minimize it. The site and situation of the location of the population center of Texas suggests that it is an ideal location for hotel investment, if minimizing travel for all Texan’s is a criteria for site selection. The
selection by Apple Computer of Round Rock in Williamson County as the site for their new factory has merit beyond such vicissitudes as abatement incentives, in that, being close to the state’s population center, it minimizes travel distances for all those visiting the plant and for deliveries from the plant.

The Texas economy is moving from a material-intensive to an information-intensive base; from a mechanical model, with its roots in mechanical energy, to the biological model, whose antecedents lie in information. How will this transformation affect the urban cadastre of Texas? From evidence on the location of the center of population of Texas, especially its location for the past forty years, the import is clear. With the population of Texas predicted to be 22.3 million by the year 2026, which maybe an underestimation, given Texas’s large 1990 population of 17 million, this population will be absorbed into the state’s present settlement pattern in a manner that will not affect it substantially, and neither consequently that of the location of the center of population of Texas.

Acknowledgements

Appreciation is extended to Mr. Frank Brazile for the preparation of Figure 1.

Literature Cited


WEIGHT ESTIMATION FOR AXIS, FALLOW, SIKA AND WHITE-TAILED DEER IN TEXAS

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Abstract.—Predictive equations provide wildlife managers and sportsmen with a practical and reliable estimate of deer weight. These equations have not been reported for axis (Axis axis), fallow (Dama dama), sika (Cervus nippon), or white-tailed deer (Odocoileus virginianus) in Texas. To address this need, the relationships between heart girth, live weight, dressed weight, and carcass weight were assessed for these cervid species in central Texas. Separate predictive equations were required for each species, age class, and season. General models using heart girth to provide an estimate of weight had $R^2$ values of 0.76, 0.75, and 0.75 for live weight, dressed weight, and carcass weight, respectively. General models using dressed weight to predict live weight and using live weight to predict carcass weight had $R^2$ values of 0.89 and 0.83, respectively.

Predictive equations based on heart girth or partial body weight provide a simple and reliable estimate of deer weight. The low cost and convenience of weight equations makes them practical for use by wildlife managers and sportsmen (Smart et al. 1973).

Viable populations of non-native deer species are present in Texas and offer a popular sporting alternative to indigenous big game. Axis, fallow, and sika deer are the most common species of exotic deer present on Texas rangelands (Traweek 1989). However, weight estimation equations have not been reported for these species nor for native white-tailed deer in the Edwards Plateau Region of Texas. The objectives of this study were to test for effects of season, age, and species on regression models for body weights of axis, fallow, sika, and white-tailed deer and to develop predictive equations of body weight for each species.

Study Area and Methods

Deer were harvested on four privately owned ranches located in Kerr and Real Counties, Texas during two winter (15 December 1987-15 January 1988 and 15 December 1988-15 January 1989) and two summer (15 July 1988-15 August 1988 and 15 July 1989-15 August 1989) sampling periods. These ranches were predominantly rangeland used for
Table 1. Linear regression equations developed to estimate live weight from heart girth for axis, fallow, sika, and white-tailed deer in Texas, 1987-89.

<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>Season</th>
<th>n</th>
<th>(\bar{x})</th>
<th>SE</th>
<th>Equation bc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Axis</td>
<td>Adult &amp;</td>
<td>Summer</td>
<td>55</td>
<td>44.1</td>
<td>3.6</td>
<td>(Y = -14.38 + 0.08(HG))</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>Winter</td>
<td>46</td>
<td>46.8</td>
<td>3.0</td>
<td>(Y = -2.67 + 0.07(HG))</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>Winter</td>
<td>10</td>
<td>39.5</td>
<td>3.7</td>
<td>(Y = -2.67 + 0.06(HG))</td>
</tr>
<tr>
<td>Fallow</td>
<td>Adult</td>
<td>Summer</td>
<td>38</td>
<td>37.1</td>
<td>4.1</td>
<td>(Y = -22.02 + 0.08(HG))</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td></td>
<td>42</td>
<td>38.0</td>
<td>2.6</td>
<td>(Y = -10.31 + 0.07(HG))</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
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<td>16</td>
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<td>2.9</td>
<td>(Y = -20.47 + 0.08(HG))</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td></td>
<td>4</td>
<td>33.8</td>
<td>2.8</td>
<td>(Y = -8.75 + 0.06(HG))</td>
</tr>
<tr>
<td>Sika</td>
<td>Adult &amp;</td>
<td>Summer</td>
<td>44</td>
<td>37.1</td>
<td>3.7</td>
<td>(Y = -20.46 + 0.08(HG))</td>
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<tr>
<td></td>
<td>Subadult</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>Winter</td>
<td>40</td>
<td>39.1</td>
<td>3.3</td>
<td>(Y = -8.75 + 0.07(HG))</td>
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<tr>
<td></td>
<td>Subadult</td>
<td>Winter</td>
<td>6</td>
<td>33.4</td>
<td>2.7</td>
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<tr>
<td>Whitetail</td>
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<td>Summer</td>
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<td>34.5</td>
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<td>(Y = -22.88 + 0.09(HG))</td>
</tr>
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<td>2.7</td>
<td>(Y = -11.17 + 0.07(HG))</td>
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<td></td>
<td>Subadult</td>
<td>Summer</td>
<td>2</td>
<td>24.5</td>
<td>2.7</td>
<td>(Y = -20.46 + 0.08(HG))</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td></td>
<td>3</td>
<td>27.8</td>
<td>0.2</td>
<td>(Y = -8.75 + 0.06(HG))</td>
</tr>
</tbody>
</table>

a Standard error of the estimate.

b Based on the general model \(Y = -8.745 + 0.058(HG) + 6.078(\text{Axis}) - 11.714(\text{Summer}) - 1.564(\text{Fallow*Adult}) - 2.421(\text{Whitetail*Adult}) + 0.007(\text{Adult*Girth}) + 0.018(\text{Summer*Girth}) - 0.003(\text{Axis*Summer*Adult*Girth}) + 0.003(\text{Whitetail*Summer*Adult*Girth}) \). \(R^2 = 0.7615\), Adj. \(R^2 = 0.7561\), N = 403, F = 139.5.

c \(Y = \) live weight in kg, HG = heart girth in mm.

d Too few observations to calculate SE.

The production of domestic livestock and wildlife and were characteristic of the Edwards Plateau Region (Butts et al. 1982; Landers 1987). Body weights and heart girth measurements were recorded for 111 axis, 100 fallow, 90 sika, and 102 white-tailed deer. All deer were female and classified as either subadult (1.0-1.5 years-old) or adult (> 1.5 years-old) based on tooth eruption and wear criteria (Severinghaus 1949; Graf & Nichols 1966; Chaplin & White 1969; Duff 1969).

A linear measurement of heart girth (Smart et al. 1973) using a flexible steel tape and recorded to the nearest 0.5 cm was taken with the deer lying on its side prior to evisceration. Live weight, defined as the weight of a recently harvested deer minus blood loss from the gunshot wound to the head, was measured using a spring scale. An electronic scale was used to determine carcass weight, defined as the weight of the eviscerated deer minus the head, hide, and feet. The combined weight of the head, hide, and feet was then measured using a spring scale and added to the carcass weight to arrive at the field dressed weight.
Table 2. Linear regression equations developed to estimate dressed weight from heart girth for axis, fallow, sika, and white-tailed deer in Texas, 1987-89.

| Species | Age      | Season | n  | X  | SE | Equation  
|---------|----------|--------|----|----|----|-----------------------------------------------
| Axis    | Adult    | Summer | 45 | 30.1 | 2.2 | Y = -15.11 + 0.06(HG) |
|         | Adult    | Winter | 56 | 28.5 | 1.7 | Y = -13.95 + 0.06(HG) |
|         | Subadult | Winter | 10 | 24.6 | 2.9 | Y = -13.95 + 0.05(HG) |
| Fallow  | Adult    | Summer | 38 | 21.7 | 2.4 | Y = -17.33 + 0.06(HG) |
|         | Adult    | Winter | 42 | 22.7 | 2.2 | Y = -16.18 + 0.05(HG) |
|         | Subadult | Combined | 20 | 19.4 | 1.6 | Y = -13.95 + 0.05(HG) |
| Sika    | Adult    | Summer | 37 | 23.6 | 2.6 | Y = -15.11 + 0.06(HG) |
|         | Adult & Subadult | Winter | 53 | 23.8 | 2.7 | Y = -8.75 + 0.07(HG) |
| Whitetail | Adult | Summer | 47 | 21.9 | 2.0 | Y = -12.44 + 0.05(HG) |
|         | Adult & Subadult | Winter | 55 | 22.3 | 2.1 | Y = -11.28 + 0.05(HG) |

a Standard error of the estimate.

b Based on the general model Y = - 13.953 + 0.048(HG) + 2.669 (Whitetail) - 2.223 (Fallow*Adult) - 1.156 (Summer*Adult) + 0.004 (Adult*Girth) + 0.003 (Summer*Girth) + 0.005 (Axis*Girth) - 0.004 (Whitetail*Adult*Girth). R^2 = 0.7543, Adj. R^2 = 0.7493, N = 403, F = 151.2.

c Y = dressed weight in kg, HG = heart girth in mm.

d This equation also represents axis subadults during the summer.

Scales were calibrated with the electronic scale, prior to each weighing session, and all weights were recorded to the nearest 0.45 kg.

Statistical analyses were performed with the PC version of the computer program SHAZAM (White et al. 1988) on an IBM PC-AT. Linear regression equations were developed describing the weight-girth and weight-weight relationships. Differences among age, season, species and the various interaction terms in the regression equations were tested with the creation of dummy variables (Leistritz 1973).

Results

Coefficient of determination (R^2) values suggested most of the variability in our data were accounted for in the various regression models. General models using heart girth to provide an estimate of weight had R^2 values of 0.76, 0.75, and 0.75 for live weight, dressed weight, and carcass weight, respectively. General models using dressed weight to predict live weight and using live weight to predict carcass weight had R^2 values of 0.89 and 0.83, respectively.

Equations developed to estimate live weight from heart girth (Table 1) varied by age and season. For each species, the live weight to girth
Table 3. Linear regression equations developed to estimate carcass weight from heart girth for axis, fallow, sika, and white-tailed deer in Texas, 1987-89.

<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>Season</th>
<th>n</th>
<th>$\bar{X}$</th>
<th>SE $^a$</th>
<th>Equation $^{bc}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Axis</td>
<td>Adult</td>
<td>Summer</td>
<td>45</td>
<td>24.2</td>
<td>1.9</td>
<td>$Y = -13.24 + 0.05(HG)$</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>Winter</td>
<td>46</td>
<td>23.4</td>
<td>1.6</td>
<td>$Y = -14.19 + 0.05(HG)$</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>Summer</td>
<td>10</td>
<td>19.8</td>
<td>1.8</td>
<td>$Y = -14.95 + 0.05(HG)$</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>Winter</td>
<td>10</td>
<td>19.6</td>
<td>2.6</td>
<td>$Y = -15.91 + 0.05(HG)$</td>
</tr>
<tr>
<td>Fallow</td>
<td>Adult &amp;</td>
<td>Summer</td>
<td>54</td>
<td>15.9</td>
<td>2.1</td>
<td>$Y = -10.22 + 0.04(HG)$</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult &amp;</td>
<td>Winter</td>
<td>46</td>
<td>16.8</td>
<td>2.1</td>
<td>$Y = -11.18 + 0.04(HG)$</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sika</td>
<td>Adult &amp;</td>
<td>Summer</td>
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<td>17.7</td>
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<td>$Y = -17.07 + 0.05(HG)$</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Adult &amp;</td>
<td>Winter</td>
<td>46</td>
<td>18.8</td>
<td>2.3</td>
<td>$Y = -18.03 + 0.05(HG)$</td>
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<td></td>
<td>Subadult</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whitetail</td>
<td>Adult &amp;</td>
<td>Summer</td>
<td>49</td>
<td>17.2</td>
<td>1.7</td>
<td>$Y = -15.98 + 0.05(HG)$</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult &amp;</td>
<td>Winter</td>
<td>53</td>
<td>17.6</td>
<td>1.8</td>
<td>$Y = -16.93 + 0.05(HG)$</td>
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<tr>
<td></td>
<td>Subadult</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Standard error of the estimate.

$^b$ Based on the general model $Y = -18.025 + 0.049\text{ (HG)} + 2.119\text{ (Axis)} + 6.850\text{ (Fallow)} + 1.094\text{ (Whitetail)} + 0.953\text{ (Summer)} + 1.718\text{ (Axis*Adult)} - 0.012\text{ (Fallow*Girth)}$. $R^2 = 0.7505$, Adj. $R^2 = 0.7460$, $N = 403$, $F = 169.7$.

$^c$ $Y =$ carcass weight in kg, HG = heart girth in mm.

The relationship was different between age-classes during winter requiring separate equations for adults and subadults. Age-specific equations were needed for fallow and white-tailed deer in the summer but not for axis or sika deer.

The dressed weight of a deer can be estimated from a linear heart girth measurement (Table 2). Separate equations were required for axis, fallow, sika, and whitetail adults harvested during summer. However, sika and whitetails each showed little variation in the dressed weight to girth relationship among adults harvested during the winter or subadults in either season. Age-related variation was apparent for axis and fallow deer.

The relationship of carcass weight to heart girth (Table 3) observed for axis, sika, and white-tailed deer differed from that of fallow deer; however, none of the species showed an age or season effect on this relationship. Seasonal variation in intercept existed; therefore, separate equations in summer and winter were needed for fallow, sika, and white-tailed deer. Four equations were necessary for axis deer because
Table 4. Linear regression equations developed to estimate live weight from dressed weight for axis, fallow, sika, and white-tailed deer in Texas, 1987-89.

<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>Season</th>
<th>n</th>
<th>X</th>
<th>SE</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Axis</td>
<td>Adult</td>
<td>Summer</td>
<td>45</td>
<td>45.7</td>
<td>2.3</td>
<td>Y = 7.20 + 1.28(DW)</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>Winter</td>
<td>46</td>
<td>46.8</td>
<td>2.1</td>
<td>Y = 13.98 + 1.12(DW)</td>
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<td></td>
<td>Subadult</td>
<td>Summer</td>
<td>10</td>
<td>37.1</td>
<td>1.0</td>
<td>Y = 7.20 + 1.18(DW)</td>
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<tr>
<td></td>
<td>Subadult</td>
<td>Winter</td>
<td>10</td>
<td>39.5</td>
<td>2.3</td>
<td>Y = 13.98 + 1.02(DW)</td>
</tr>
<tr>
<td>Fallow</td>
<td>Adult</td>
<td>Summer</td>
<td>38</td>
<td>37.1</td>
<td>3.3</td>
<td>Y = 8.54 + 1.31(DW)</td>
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<tr>
<td></td>
<td>Adult</td>
<td>Winter</td>
<td>42</td>
<td>38.0</td>
<td>2.5</td>
<td>Y = 15.31 + 1.01(DW)</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>Summer</td>
<td>16</td>
<td>29.5</td>
<td>1.9</td>
<td>Y = 7.20 + 1.21(DW)</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>Winter</td>
<td>4</td>
<td>33.8</td>
<td>1.8</td>
<td>Y = 13.98 + 0.91(DW)</td>
</tr>
<tr>
<td>Sika</td>
<td>Adult</td>
<td>Summer</td>
<td>37</td>
<td>38.2</td>
<td>2.3</td>
<td>Y = 7.20 + 1.31(DW)</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>Winter</td>
<td>40</td>
<td>39.1</td>
<td>2.0</td>
<td>Y = 13.98 + 1.01(DW)</td>
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<td></td>
<td>Subadult</td>
<td>Summer</td>
<td>7</td>
<td>31.5</td>
<td>2.3</td>
<td>Y = 7.20 + 1.21(DW)</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>Winter</td>
<td>6</td>
<td>33.4</td>
<td>1.9</td>
<td>Y = 13.98 + 0.91(DW)</td>
</tr>
<tr>
<td>Whitetail</td>
<td>Adult</td>
<td>Summer</td>
<td>47</td>
<td>34.5</td>
<td>1.9</td>
<td>Y = 0.50 + 1.55(DW)</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>Winter</td>
<td>50</td>
<td>34.3</td>
<td>1.8</td>
<td>Y = 7.27 + 1.19(DW)</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>Summer</td>
<td>2</td>
<td>24.5</td>
<td>1.9</td>
<td>Y = 0.50 + 1.39(DW)</td>
</tr>
<tr>
<td></td>
<td>Subadult</td>
<td>Winter</td>
<td>3</td>
<td>27.8</td>
<td>0.6</td>
<td>Y = 7.27 + 1.09(DW)</td>
</tr>
</tbody>
</table>

a Standard error of the estimate.
b Based on the general model Y = 13.975 + 0.906 (DW) - 6.705 (Whitetail) - 6.773 (Summer) + 1.337 (Fallow*Adult) + 0.103 (Adult*DW) + 0.115 (Axis*DW) + 0.184 (Whitetail*DW) + 0.300 (Summer*DW) - 0.141 (Axis*Summer*DW) + 0.059 (Whitetail*Adult*Summer*DW). R² = 0.8855, Adj. R² = 0.8825, N = 403, F = 303.0.
c Y = live weight in kg, DW = dressed weight in kg.
d Too few observations to calculate SE.

of age- and season-related variation in intercept terms.

Equations designed to predict live weight from dressed weight (Table 4) and carcass weight from live weight (Table 5) reflect age-related differences for axis, fallow, sika, and white-tailed deer. Variation in the live weight to dressed weight relationship also occurred by season for all species. Only axis and fallow deer required season-specific equations to estimate carcass weight from a live weight measurement.

Discussion

Strong correlation among body weights and heart girth has been reported for white-tailed deer in the southeastern United States (Smart et al. 1973; Urbston et al. 1976; Weckerly et al. 1987). Results of this study verify this relationship for axis, fallow, sika, and white-tailed deer in Texas with standard errors for specific estimates similar to those reported for white-tailed deer in Illinois (Roseberry & Klimstra 1975)
Table 5. Linear regression equations developed to estimate carcass weight from live weight for axis, fallow, sika, and white-tailed deer in Texas, 1987-89.

<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>Season</th>
<th>n</th>
<th>( \bar{X} )</th>
<th>SE (^a)</th>
<th>Equation (^bc)</th>
</tr>
</thead>
<tbody>
<tr>
<td>轴</td>
<td>成年</td>
<td>夏季</td>
<td>45</td>
<td>24.2</td>
<td>1.3</td>
<td>( Y = 0.57 + 0.52(LW) )</td>
</tr>
<tr>
<td>轴</td>
<td>成年</td>
<td>冬季</td>
<td>46</td>
<td>23.4</td>
<td>1.6</td>
<td>( Y = 0.57 + 0.49(LW) )</td>
</tr>
<tr>
<td>轴</td>
<td>幼年</td>
<td>夏季</td>
<td>10</td>
<td>19.8</td>
<td>1.1</td>
<td>( Y = -1.46 + 0.57(LW) )</td>
</tr>
<tr>
<td>轴</td>
<td>幼年</td>
<td>冬季</td>
<td>10</td>
<td>19.6</td>
<td>1.5</td>
<td>( Y = -1.46 + 0.54(LW) )</td>
</tr>
<tr>
<td>落</td>
<td>成年</td>
<td>夏季</td>
<td>38</td>
<td>16.3</td>
<td>1.8</td>
<td>( Y = 2.97 + 0.36(LW) )</td>
</tr>
<tr>
<td>落</td>
<td>成年</td>
<td>冬季</td>
<td>42</td>
<td>16.9</td>
<td>2.2</td>
<td>( Y = -1.46 + 0.36(LW) )</td>
</tr>
<tr>
<td>落</td>
<td>幼年</td>
<td>夏季</td>
<td>16</td>
<td>14.9</td>
<td>1.5</td>
<td>( Y = 2.97 + 0.53(LW) )</td>
</tr>
<tr>
<td>落</td>
<td>幼年</td>
<td>冬季</td>
<td>4</td>
<td>15.3</td>
<td>2.0</td>
<td>( Y = -1.46 + 0.53(LW) )</td>
</tr>
<tr>
<td>喜</td>
<td>成年</td>
<td>合计</td>
<td>77</td>
<td>18.5</td>
<td>1.8</td>
<td>( Y = -1.46 + 0.52(LW) )</td>
</tr>
<tr>
<td>喜</td>
<td>幼年</td>
<td>合计</td>
<td>13</td>
<td>17.0</td>
<td>2.4</td>
<td>( Y = -1.46 + 0.57(LW) )</td>
</tr>
<tr>
<td>白尾</td>
<td>成年</td>
<td>合计</td>
<td>97</td>
<td>17.5</td>
<td>1.3</td>
<td>( Y = -0.27 + 0.52(LW) )</td>
</tr>
<tr>
<td>白尾</td>
<td>幼年</td>
<td>合计</td>
<td>5</td>
<td>14.4</td>
<td>0.9</td>
<td>( Y = -1.46 + 0.57(LW) )</td>
</tr>
</tbody>
</table>

\(^a\) Standard error of the estimate.
\(^b\) Based on the general model \( Y = -1.459 + 0.567(LW) + 4.432(\text{Fallow}\times\text{Summer}) + 2.025(\text{Axis}\times\text{Adult}) + 1.194(\text{Whitetail}\times\text{Adult}) - 0.050(\text{Adult}\times\text{LW}) - 0.031(\text{Axis}\times\text{LW}) - 0.037(\text{Fallow}\times\text{LW}) + 0.031(\text{Axis}\times\text{Summer}\times\text{LW}) - 0.123(\text{Fallow}\times\text{Summer}\times\text{LW}) \). \( R^2 = 0.8256 \), Adj. \( R^2 = 0.8216 \), \( N = 403 \), \( F = 206.7 \).
\(^c\) \( Y = \) carcass weight in kg, \( LW = \) live weight in kg.

Analyses revealed the need for separate weight estimation equations among cervid species, age classes, and seasons in the Edwards Plateau Region of Texas. Although separate regression equations presented in this study have been determined to be statistically different (Tables 1-5), biologically significant differences may not exist in cases where both intercepts and slopes are very similar.

Models were developed using data collected exclusively from female deer and, therefore, may or may not be applicable for males of the respective species (Smart et al. 1973; Weckerly et al. 1987). Also, the Edwards Plateau Region of central Texas supports a very dense deer population. Because deer weights may be population specific, caution should be used when applying these predictive equations to other deer populations.

Acknowledgments

We thank the owners and managers of the Bowman, Johnson, Two-Dot, and Y.O. ranches for their hospitality and assistance. We would also like to thank the Texas Wild Game Cooperative, All That’s Deer,
Inc., J. J. Jackley, M. Bailey, and several students at Texas Tech University for their assistance in data collection and R. S. Lutz, L. M. Smith, and J. J. Jackley for reviewing the manuscript. This research was supported by the Exotic Wildlife Association, Texas Tech University, the Houston Livestock Show and Rodeo, and various private landowners. This manuscript is Texas Tech University, College of Agricultural Sciences Contribution T-4-590.

Literature Cited

LATE PREHISTORIC SNAKES OF E. V. SPENCE AND O. H. IVIE RESERVOIR BASINS OF COKE, COLEMAN, CONCHO, AND RUNNELS COUNTIES, TEXAS

Okla W. Thornton, Jr. and J. R. Smith
Colorado River Municipal Water District,
Ivie Reservoir Field Office, HCR 82, Box 4B
Leaday, Texas 76888

Abstract.—Eighteen fossilized snake vertebrae representing at least four different genera were recovered from the archaeological surveys of four prehistoric campsites along the Colorado River of west-central Texas. The sites are now inundated by E.V. Spence and O.H. Ivie reservoirs. All fossils examined represent extant forms that are currently present in this region of Texas. The occurrence of these species indicates that the prehistoric climate in this area was very similar to that of today. The incompleteness of the fossils and their proveniences suggests that they were part of the aboriginals diet.

Four snake genera are identified from four different prehistoric campsites along the Colorado River, Texas. Although few in number, the vertebrae have zooarchaeological significance. Because of their present-day habitat preferences, zoogeographic distribution, and the convergence of three physiographic regions in or near the fossil sites, the vertebrae found at these prehistoric campsites demonstrate a dietary use of snakes by early native Americans. Many archaeological investigations (Ruecking 1953; Sjoberg 1953; Newcomb 1961; Williams-Dean 1978; Steele & Mokry 1985; Shafer 1986; Steele & Hunter 1986; Steele 1986a; 1986b; Hellier et al. in press) have reported snake consumption but there appears to be little interest in the identification of those species which were being consumed. There are probably numerous snake bones stored in archeology holdings that are never examined in a critical manner (Parmely pers. comm.). It would appear that to fully understand the dietary habits of early native Americans, archaeologists would need to determine what types of snakes were being consumed by native Americans.

Study Areas

E. V. Spence Reservoir.—The Sand Creek archaeological site (41CK79) is within E. V. Spence Reservoir basin, Coke County, Texas (Fig. 1). The Robert Lee Dam, which impounds the reservoir, is 48 km NNW of San Angelo. The prehistoric campsite where the vertebrae were recovered is 21 km NW of the dam on a 9 m terrace of Sand
Figure 1. E. V. Spence and O. H. Ivie reservoir locations along the upper Colorado River basin of west-central Texas.

Creek about 305 m from the bank of the Colorado River (Shafer 1971). The elevation of the Sand Creek site is between 576-579 m above mean sea level (msl). The site is within the Mesquite Plains, a subregion of the Rolling Plains (Smeins & Slack 1982).

**O. H. Ivie Reservoir.**—Three prehistoric sites, now inundated by O. H. Ivie Reservoir, are located within a 6.1 km radius of the confluence of the Colorado and Concho Rivers (Fig. 1). The S. W. Freese Dam, which impounds the reservoir, is 26 km downstream from this confluence. The reservoir is approximately 74 km ENE of San Angelo. Site 41CN19 is 6.5 km north of the Freese Dam service spillway (Coleman County) on a left-bank terrace above the Colorado River in proximity to an unnamed ravine through which a perennial spring flowed. Site 41CC131 is situated 7.8 km NW of Freese Dam (Concho County) on a right-bank terrace above the Concho River in proximity to an unnamed intermittent stream traversing a ravine. Site 41RN169 is 15.5 km NW of Freese Dam (Runnels County) on the left-bank of the Colorado River, about 228 m upstream on Rocky Branch, an intermittent stream. The elevation of the sites ranges from 457-469 m above msl. A detailed description of each site is presented by Lintz et al. (1993).
Methods and Materials

Identifications were made by comparing the fossil vertebrae with modern reference skeletons in the collection of the senior author. Drawings of fossilized vertebrae from published literature were also reviewed to aid in comparisons and identifications. Catalog or lot and site numbers (in parentheses) refer to the field specimen and site collections (trinomial code), respectively, of the Texas Archeological Research Laboratory (TARL) and Mariah Associates, Inc. Radiocarbon (Carbon-14) dates are based upon communitive charcoal recovered at each site. The fossil specimens are maintained at the Texas Archeological Research Laboratory. The classification system follows Dowling & Duellman (1976) with standard scientific names from Collins et al. (1978).

Results

The following species accounts include specimens of at least four different genera assigned to the families Colubridae and Viperidae. Drawings of fossil specimens examined during the course of this study are presented in Figure 2.

*Elaphe obsoleta* (Say)

*Material examined.*—One large trunk vertebra (FS 114, 41CC131; Fig. 2A-C) was found 130 cm below the surface north of the deep gully, but insufficient diagnostic artifacts were found with the vertebra to allow a relative age assignment. The large size of the vertebra indicates a mature individual. The neural arch is not highly vaulted and the subcentral ridges are relatively deep. *Elaphe obsoleta* is presently widespread in the eastern two-thirds of the state while the study area is near the western range limit (Dixon 1987). *Elaphe obsoleta* lives in a variety of habitats, but within the basin it is typically found in wooded stream valleys and rocky canyons (Conant & Collins 1991).

*Masticophis* sp. or *Coluber* sp. (indeterminable)

*Material examined.*—Eight trunk vertebrae (one FS 566.1, four FS 685.1, 41CN19; two FS 1218.1 (Fig. 2D-F), one FS 114, 41CC131) and two cervical vertebrae (one FS 1224.1, 41CC131; one FS 685.1, 41CN19) are identified as those of either *Masticophis* or *Coluber*. Vertebrae of *Masticophis* are inseparable from those of *Coluber* (cf. Holman...
Figure 2. Fossil vertebrae of *Elaphe obsoleta* (A-C), *Masticophis/Coluber* sp. indet. (D-F), *Thamnophis* sp. (G-I), *Crotalus* sp. (J-O), each shown in dorsal, posterior and lateral views respectively. Scale is 1.0 cm.
1979; 1981; Parmley 1986; 1988a; 1988b; 1990). Though non-distinguishable, these vertebrae (FS 114, FS 1224.1, FS 566.1, FS 685.1, and FS 1218.1) exhibit the following characters typical of these genera: general shape long and constricted medially; well developed epizygapophyseal spines; thin, long neural spine; thin, relatively uniform in width hemal keel; strong posterior neural spine overhang; and high, domed neural arch. *Masticophis/Coluber* vertebrae are the most common elements recovered at the sites. *Masticophis flagellum, Masticophis taeniatus*, and *Coluber constrictor* currently occur sympatrically within the reservoir area (Dixon 1987). *Coluber constrictor* inhabits fields, grasslands, brushlands, and open woodlands; *M. flagellum* frequents grasslands, mesquite savannahs, arid brushlands, and many other more or less open habitats; and *M. taeniatus* prefers rocky breaks and stream valleys (Conant & Collins 1991).

Of the ten vertebrae, all post- and prezygapophyseal processes were damaged. One trunk vertebra (FS 566.1) of an adult snake was found 160-170 cm below the surface and shows evidence of being burned and slightly weathered. Four trunk and one cervical vertebrae (FS 685.1) were found 190-200 cm below the datum, and they appear to be from a single individual and show moderate weathering and signs of burning. The cervical vertebra was badly damaged and burned. Two trunk vertebrae (FS 1218.1) were found 40-50 cm below the surface. These specimens indicate two individuals with minute signs of weathering, however, both clearly show signs of being burned. One cervical vertebra (FS 1224.1) was found 190-200 cm below the datum. This specimen was slightly weathered with signs of being burned. One trunk vertebra (FS 114) was found 130 cm below the surface. It appears to be from a moderately sized individual, with some weathering and signs of being burned. Carbon-14 dates associated with these vertebrae are: FS 566.1 and FS 685.1, associated materials and stratigraphic data suggests site utilization between A.D. 600 to 1050; FS 1218.1 and FS 1224.1, material remains suggest an age span of A.D. 1000 to 1300; and FS 114, no dates are associated because insufficient diagnostic artifacts were found to provide a relative age for this specimen.

*Thamnophis* sp.

*Material examined.*—One trunk vertebra (Lot 133, 41CK79; Fig. 2G-I) was found 22.9-30.5 cm below the surface in association with rich cultural deposits including freshwater mussel shell, flint, and hearthstones. Artifacts recovered suggest a time span of about A.D. 800
to 1600 (1100 to 200 YBP). This specimen appears to be *Thamnophis*, because of its elongated shape. However, it could be *Nerodia harteri paucimaculata*, although the neural arch is not quite the same. Nonetheless, the hypapophysis of *Thamnophis* is similar to *N. harteri* (Parmley pers. comm.), therefore, the possibility that this specimen could be *N. harteri paucimaculata* cannot be ruled out. At any rate, lack of adequate *N. harteri* reference skeletons make a positive identification difficult to impossible. Both *Thamnophis marcianus marcianus* and *Thamnophis proximus rubrilineatus* presently occur in or near the site. *Thamnophis marcianus marcianus* is widely distributed in the arid Southwest and *T. proximus rubrilineatus* occurs in central to west-central Texas. Both seldom stray far from streambeds, springs, or other places where water may be present (Conant & Collins 1991), however, this site occurs at the western extremes of *N. harteri paucimaculata* range (Dixon 1987).

*Crotalus* sp.

*Material examined.*—Five trunk vertebrae (FS 141.1, 41CC131; Lot 115 (n=2), Lot 77, and Lot 231, 41CK79) are identified as *Crotalus*. Vertebra FS 141.1(Fig.2J-L) was found 170 cm below the surface during the testing phase in TP 4, north of the deep gully. No dates are associated and insufficient diagnostic artifacts were found to provide a relative age for this specimen. The vertebra appeared to be that of a moderately sized individual with signs of burning. FS 141.1 was identified as *Crotalus* sp. indet., in that it is rather short and wide, the zygosphene is thick, and the hypapophysis base is thick like a viperid. The remaining four trunk vertebra (Lot 115, Lot 77, and Lot 231) are from moderately sized rattlesnakes and more associated with artifacts suggesting a time span of about A.D. 800 to 1600. Two large vertebrae (Lot 115) were found 22.9-30.5 cm below the surface during the recovery phase in Level 4. All were charred and extremely fragmented. One vertebra (Lot 77) was found 15.2- 22.9 cm below the datum during the recovery phase in Level 3, and one vertebra (Lot 231) was found 30.5-38.1 cm below the surface during the recovery phase in Level 5. The overall shape (squareness), robustness, and low neural arch of the vertebra are characteristic of the genus *Crotalus*. Because of the poor preservation and fragmentation of the specimens, allocation to species cannot be ascertained.

One trunk vertebra (FS 692.1, 41RN169; Fig. 2M-O) was found 70-80 cm below the surface within the central pit of a burned rock oven.
This vertebra is relatively well preserved and appears to be either *C. atrox* or *C. viridis*. Both species presently occur at or near the site, but the single vertebra is indistinguishable from either species. In fact, *Crotalus molossus* may occur there as well. This vertebra is rather large indicating a large, adult snake with signs of slight weathering and being burned. The artifacts and C-14 dates support use of the oven between A.D. 700 and 1200. The specific identification of *Crotalus* vertebrae presents special problems that are yet to be worked out (Holman 1981; Parmley 1986; 1988a; 1990). Parmley (1988a) states that fossil vertebrae of *C. atrox* and *C. viridis* of comparable size cannot be distinguished. He further states that specific identification of isolated *Crotalus* vertebrae has never been satisfactorily analyzed, and it is possible that *Crotalus* vertebrae are not diagnostic at the species level. The same problem exists for *C. molossus*. Both *C. viridis* and *C. molossus* are medium-sized rattlesnakes (range 89-114 cm, record 144.8 cm; 76-106.7 cm, record 125.7 cm, respectively) compared to *C. atrox* (range 76-183 cm, record 213 cm) (Conant & Collins 1991). All three species presently occur at or near the fossil sites (Dixon 1987).

**Discussion**

The purpose of analyzing the few herpetofaunal remains recovered from 41CN19, 41CC131, 41RN169 and 41CK79 was twofold. First, the prehistoric occupation sites where the fossils were collected are in proximity to the mainstem stream riffles of the Colorado River. With the knowledge that the aboriginal inhabitants utilized riverine based resources (Carlson et al. 1982), the question was asked whether natracines, specifically, the Concho water snake (*N. harteri paucimaculata*), occurred in the region prior to European occupation. Second, the opportunity to report the dietary use of prehistoric snakes by early native Americans.

More than 50,000 bone specimens were recovered during the archaeological testing and data recovery within the Ivie Reservoir basin. A majority of the bone specimens recovered represent small-to large-sized animals, many of which persist in or near the area today. Only a few of these bones were attributed to avifaunal, ichthyofaunal, and herpetofaunal assemblages (Lintz et al. 1993). The 13 snake vertebrae recovered represents only 0.03% of the total bones recovered.

A total of 147 vertebrate bone specimens were recovered from the Spence Reservoir site, and snake vertebrae represented only 3.4% of
that total. A review of earlier studies (Carlson et al. 1982; Steele & DeMarcay 1985; Steele & Mokry 1985; Steele 1986a; 1986b; Steele & Hunter 1986; Hellier et al. in press) indicates that numerically the herpetofaunal portions of the assemblages are poorly represented. Steele (1986b) explains this apparent disparity by suggesting that mammals constitute the largest faunal remains because of a greater utilization by early man. His reasons were: (1) the bones of the other classes are smaller and more fragile, therefore more subject to destruction and loss; and (2) when the amount of meat contributed by each class of vertebrates is considered, the mammals are the most important, since most species of mammals are considerably larger than other vertebrates. Driver (1969) indicated that when large game animals were scarce, the hunters and gatherers relied more on rodents, reptiles, and insects. However, Steele & Mokry (1985) state that faunal utilization involved all classes and sizes of vertebrates, and furthermore, there is no evidence indicating any fauna was favored to the exclusion of others.

Another question to be addressed is whether the fossils recovered at human habitation sites were intrusively or consumptively deposited. Steele & DeMarcay (1985) lists two criteria with which one can, with assurance, make these decisions. First, the disarticulation of the skeleton and its overall incompleteness represented by single bones or bone fragments indicates probable consumption. Second, a skeleton found articulated and generally complete, indicates an intrusive element. However, they admit one should be judicious when drawing conclusions based upon faunal remains. Nonetheless, the archaeological evidence suggests that when faunal remains are recovered disarticulated, few in number, and within the tight stratigraphic context directly associated with an archaeological habitation, then the taxon represented was most likely consumed. Bones recovered from hearth areas and showing signs of burning (charring) and disarticulation clearly point to human involvement, particularly dietary consumption (Shafer 1986). Furthermore, through coprolite examination Williams-Dean (1978) confirmed that snakes were consumed.

A complete review of the available literature, concerning the dietary use of natracines by prehistoric peoples was not attempted, however, one example was found. Steele (1986b) examined the vertebrate remains recovered from a Late Prehistoric site (ca. A.D. 1250-1500) and identified four snake genera, one being a *Nerodia* (sp. indet.). He noted that five aquatic taxa, including the water snake, indicated the presence of a nearby stable aquatic habitat.
If colubrines and crotalines have consistently been reported as probable, if not actual food items, why then has *Nerodia* been noticeably absent. The close proximity of Prehistoric campsites to intermittent and perennial streams draining this xeric region, in conjunction with an abundance of mussel shell accumulations, clearly indicates the utilization of riverine resources. If natracines occurred here at this time, as the paleoherpetofaunal evidence attests (Holman 1981), and if the Prehistoric peoples were in somewhat of a continuous contact with this riparian habitat, why is one of the most numerous water snakes, *N. harteri paucimaculata*, (or any other water snake species) not represented in the fossil collections.

To answer this question, an analogy between two predator-prey relationships is necessary. First, Parmley (1986) examined a herpetofaunal assemblage from a sinkhole located in the karst terrain characteristic of south-central Texas. The faunal remains were primarily attributed to feeding activities of the Common Barn Owl (*Tyto alba*), although some may have entered voluntarily or simply fallen into the hole (Dalquest et al. 1969). Parmley (1986) explains the apparent lack of natracine fossils compared to the overwhelming abundance of colubrines fossils by indicating a bias in raptor selection of prey. He suggested that the woodland and grassland forms (especially colubrines) were an easier prey for the owls simply because they often forage in the open. However, aquatic forms such as natracines were usually more restricted to their habitat, hence, more protected. Second, the vast majority of the faunal remains recovered and attributed to food procurement, were diurnal creatures.

Following Parmley’s (1986) suggestion, the analogy between predators (humans or owls) becomes obvious. Furthermore, the herpetofaunal remains recovered in the cultural context strongly suggests warm weather harvesting (Steele & Hunter 1986). As diurnal temperatures increase in the summer months, natracines are known to become more crepuscular or nocturnal. Another important consideration is the medium in which the various snakes escape predation. Although the terrestrial refuges sought by escaping snakes makes it somewhat difficult for hunters to capture their prey, it can be done. Contrary to this, field experience with water snakes reveals that once they enter the water, the chance of capturing them diminishes greatly. It then becomes apparent why colubrines dominate the fossil snake assemblages in ancient campsites. First, terrestrial snakes are more numerous; second, most of the larger forms are diurnal; and third, the hunting area and it’s
resources are dominated by the arid landscape. Today in this region water is still a limited resource surrounded by the arid uplands. One could reliably conclude that the faunal assemblage, whether intrusively or culturally deposited, would reflect this ecological reality as well.

The actual dietary use of natracines in this region cannot be documented, but can be confirmed for some of the crotalid and colubrid taxa recovered. Ruecking (1953) and Sjoberg (1953) have documented the consumption of rattlesnakes by the Historic Coahuiltecan and Tonkawa Indians. Crotalids have also been documented as food items for Archaic, Prehistoric, and Late Prehistoric Indians (Newcomb 1961; Steele & Mokry 1985; Shafer 1986; Steele & Hunter 1986; Steele 1986a; 1986b; Hellier et al. in press;). Colubrids were consumed as well (Newcomb 1961; Steele & DeMarcay 1985; Steele & Mokry 1985; Shafer 1986; Steele 1986b), however, Steele & Hunter (1986) admit that the ranges in size of the snake vertebrae recovered clearly indicates that a variety of these reptiles were being harvested. Interestingly, from Post-Pleistocene hearths dated ca. 8,000 YBP, 16 species of snake were recovered ranging from large rattlesnakes to very small nonpoisonous snakes (Shafer 1986). The identified genera include *Crotalus* (prob. *C. atrox*), *Agkistrodon* (prob. *A. contortrix*), *Elaphe* (sp. indet.), *Nerodia* (sp. indet.), and *Lampropeltis* (sp. indet.). Excluding the unidentified snake species, the percentages of the remaining snakes are: crotalids, 57.1%; terrestrial colubrids, 35.8%; and aquatic natracines, 7.1%. The percentages of snake taxa recovered indicates a strong preference for crotalids, however, if indeterminate species are included the percentages are: crotalids, 44.4%; colubrids, 27.8%; indeterminate snakes, 22.2%; and natracines, 5.5%. Presently, 36 taxa of snakes occurs in or near the fossil sites (Dixon 1987). Of these, colubrids represent 83.3% and crotalids 16.7%.

Upon examination of the snake remains recovered from 41CN19, 41CC131, and 41RN169, it is apparent that these Prehistoric people were consuming *E. obsoleta*, *Crotalus* (prob. *C. atrox*), *Masticophis* (prob. *M. flagellum*), and possibly *Coluber* (prob. *C. constrictor*). This is based upon the observation that *E. obsoleta*, *C. atrox*, and *M. flagellum* occur in the area today, and they are the largest members (length and mass) of the locally occurring terrestrial or aquatic taxa. These snakes are also more commonly found than their con-specifics (*E. guttata*, *C. viridis*, *C. molossus*, and *M. taeniatus*).
Acknowledgments

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OBSERVATIONS ON COMPARATIVE GROWTH RATES AND EARLY DEVELOPMENT IN TWO LITTERS OF THE MEXICAN GROUND SQUIRREL, SPERMOPHILUS MEXICANUS (RODENTIA: SCIURIDAE)

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Abstract.—Two captive-born litters of the Mexican ground squirrel (Spermophilus mexicanus) were maintained for a period of 75 days. Body weights, and lengths of hind foot and tail of young animals were recorded at regular intervals. The first litter was characterized by individuals which grew rapidly and at very similar rates. By contrast, the second litter was characterized by an initially depressed growth rate, a partially compensatory terminal acceleration in growth, and considerable variation in individual growth rates. Observations on the timing sequences of eye-opening and juvenile and subadult molt sequences are also presented. Levels of variability in patterns and rates of growth and development suggest that these data are too preliminary to permit a full characterization for this species in regard to these aspects of growth and development.

Even for many common and widespread mammalian species, summaries in the literature of reproductive biology, growth rates, and development patterns are often sketchy and anecdotal. Further, if the data are few, the possibility exists of presenting (or perpetuating) an oversimplified view of uniformity of behavior, rates, or patterns. This was found to be true for the fox squirrel, Sciurus niger (cf. Stangl 1993).

Little is known of the reproduction, growth, and development of the Mexican ground squirrel, Spermophilus mexicanus (cf. Young & Jones 1982). The basis for general references in the literature detailing these aspects of the biology of this species (e.g. Davis & Schmidly 1994; Schmidly 1977; Young & Jones 1982) appears to be Edwards' (1946) description of a newborn litter and immature animals of unspecified age.

This study details growth rates for two captive-born litters of S. mexicanus, as measured by body weight and lengths of the tail and hind foot. Rates of development are described, and the extent of inter- and intralitter size variation is discussed.

Methods

Adult females of Spermophilus mexicanus from Haskell Cemetery, Haskell County, Texas, were housed in large glass aquariums lined with
cedar shavings and maintained on a diet of alfalfa pellets and water. Animals were kept captive for 35 days to allow sufficient time for visible manifestation of any pregnancy. Five of six adult females taken on 15 May 1993 had not been impregnated, but a single animal gave birth on 23 May to six young. Neonates were toe-clipped, weighed, and measured for greatest lengths of tail and hind foot. Weights and measurements were taken of neonates when first observed, and at five-day intervals thereafter. Observations on growth and development were recorded on a daily basis. The mother was removed from the cage after 50 days, and released at the place-of-capture. Young animals were sacrificed and prepared as study skins with skeletons at 75 days-of-age.

The same protocol outlined above was followed for seven adult females collected on 25 March 1994. The single pregnant female gave birth on 23 April to seven young. One neonate was missing on the second day and presumed to have been cannibalized. Weights and measurements were recorded for neonates, and on days 10, 15, 20, 30, 40, 50, and at 75 days-of-age, when they were sacrificed and prepared as study specimens. All voucher specimens were deposited in the Collection of Recent Mammals, Midwestern State University.

Regression analyses, ANOVAs to detect any sexual dimorphism, and t-tests for interlitter comparisons, were computed with NCSS, version 5.03 (Hintze 1990).

Results and Discussion

_Growth rates for litter one._—This litter was comprised of three males and three females. The neonates averaged 6.9 g, somewhat larger than the mean weight of 4.3 g for four animals reported by Edwards (1946), although tail and hind foot measurements were similar to his respective findings of 13.9 mm and 8.6 mm (Table 1). Individuals remained docile and were easily managed during data-recording sessions. Growth rates for each character of each age category were comparable among littermates, providing uniform patterns of growth (Fig. 1). The most striking example of individual variation was noted in weights of neonates ranging from 5.2-8.3 g, although coefficients of variation (CV) steadily decreased with age (from 17.41 to 2.76; Table 1). Increase in tail lengths and body weights were almost imperceptible after day 60, although hind foot measurements achieved adult dimensions by day 50. While other workers (Cothran 1983; Yancey et al. 1993) have described sexually dimorphic aspects of the cranium, no variation by sex was noted in this study for any character at any age category (one-way ANOVAs, P > 0.05).
Growth rates for litter two.—Five males and one female comprised this litter. Compared to the first litter, these animals became progressively wild and aggressive during handling sessions, and no attempts were made to weigh or measure living specimens after day 50. This litter showed extensive individual variation, and individuals were smaller and slower-growing than their litter one counterparts (Table 1). Initially depressed rates of weight gain and tail growth were followed by a period of rapid recovery of weight and tail dimensions between days 50 and 75. This was especially noticeable for two males, whose stunted growth rates were largely responsible for the litter’s consistently lower
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Table 1. Comparisons of descriptive statistics for weights (g) and body measurements (mm) of two captive-born litters (N = 6 for each) of *Spermophilus mexicanus* originating from Haskell County, Texas.
means of weights and measurements and higher coefficients of variation. The rate of hind foot growth more closely approximated that of litter one individuals.

Development

Edwards (1946) accurately described neonate Mexican ground squirrels as pink, blind, hairless, and marked by vibrissae and comparatively well-developed forelimbs. Members of litter one exhibited nearly parallel patterns and rates of development and comprise the basis for the following summary.

Pelage development in the species closely follows the spring molt pattern described by Goetze & Stangl (1989), which begins on the head, progresses caudally along the dorsal midline to the tail, and then advances towards the ventral midline. Although fine and sparsely distributed silky hairs were observed over the bodies of neonates, emerging guard hairs were first visible on the head after day five. The characteristic pattern of the species is visible cranially by day 10, and within three days, the rows of spots extended laterally and over the length of the dorsum. The body was essentially covered with the fine hair comprising the juvenile pelage by day 20, at which time the animals were clearly recognizable as young Mexican ground squirrels.

Eyelid development was evident by day five. Opening of the eyes signaled the beginnings of exploratory movements and serious attempts to sample solid foods. The eyes of one squirrel had opened by 22 days-of-age, and by day 24, all animals had opened their eyes. Movement was initially slow and cautious, but by day 31, the young displayed the degree of confidence and coordination in movement typical of wild-born juveniles first emerging from nest burrows. Wrestling matches became more vigorous and more frequent in occurrence. It appeared obvious that the mother would have either abandoned the young or driven them away by this time, for she rejected most attempts of the young to suckle and spent most daylight hours in the cage corner opposite of the nest.

Replacement of juvenile pelage by the darker subadult coat is indistinguishable from the adult summer pelage described by Stangl et al. (1986), and occurs in reverse of the fall molt, beginning ventrally and extending towards the dorsal midline. This process was difficult to evaluate and was evident to us only when near completion. By 75 days-of-age, only one of the animals had completed the body molt to subadult pelage. The remaining individuals still possessed the thin, pale remnants of their juvenile pelage as an irregular midline stripe from 5-40 mm
wide from head to tail. The process was more advanced among members of the second litter, where all but one animal possessed the full subadult body pelage at day 75.

Summary and Conclusions

One can only speculate how accurately these observations of one or both litters summarize early growth and development in *Spermophilus mexicanus*, or how variable these results would have been, had it been possible to assess these same litters as they developed under natural conditions.

Yet to be determined are the factors responsible for variation of rates and patterns such as those observed both within and between the two litters. No obvious differences were observed in the quality of maternal care and all squirrels were maintained on identical regimens. It is possible that the variability in individual growth rates may simply reflect the genetic variability (e.g. varying heterozygosity levels of individual squirrels). One cannot discount the possibility that *S. mexicanus* practices multiple insemination, as occurs with the closely related thirteen-lined ground squirrel, *S. tridecemlineatus* (cf. Schwagmeyer 1984). Multiple-sired litters would exhibit greater genetic variability than those fathered by a single male. Further, if the time elapsed between successful copulations is correlated with zygotic implantation events, then the gestation times would vary between littermates. Litter runts might therefore represent either inferior genotypes or minimal gestation time.

The sexual dimorphism of cranial and skeletal characters documented by Cothran (1983) and Yancey et al. (1993) from among natural populations is not evidenced in this study. Unless body measurements and weight are not sexually dimorphic, then this discrepancy may be attributed to sampling error or differential growth of the sexes beyond the squirrels’ first 75 days of life.

However the differences displayed between these two litters may be explained, the limited data presented in this study clearly illustrate the danger of attempting to characterize growth and development of a species on the basis of a single set of observations.

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Literature Cited


NEW RECORDS OF NATANT DECAPODS
(CRUSTacea: PALAEMONIDAE)
FROM THE SOUTH TEXAS COAST

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Abstract.—Two coastal water crustaceans assigned to the family Palaemonidae, Pontonia domestica Gibbes and Palaemon floridanus Chace, are reported for the first time from the south Texas coast. The occurrence of these two species in the waters of the western Gulf of Mexico is discussed relative to their currently known distributions.

The natant decapod fauna of the coastal waters of the western Gulf of Mexico remains poorly investigated. The major works of Holthuis (1951; 1952), Williams (1965; 1984) and Chace (1972) have in general surveyed those Atlantic, Caribbean and eastern Gulf of Mexico species which also range into the western Gulf. While extensive in nature, the study by Rodriguez de la Cruz (1965) examined only collections from Mexican waters and did not include the southern coast of Texas. Wood’s (1974) key to the natant decapods provides the singular most condensed listing for the Texas coast.

The following two species of natant decapods are added to those species currently known to inhabit the coastal waters of south Texas. Voucher specimens are deposited with the holdings of the National Museum of Natural History (USNM) of the Smithsonian Institution in Washington, D.C.

Pontonia domestica Gibbes 1850


Type-locality.—South Carolina.

Material Examined.—South Padre Island, Cameron County, Texas, 20 November 1976, one male and one female (USNM 325159).

Variation.—The female specimen measures 25.5 mm with a carapace length of 10 mm. The male specimen measures 23 mm with a carapace length of 9.5 mm. The male specimen agrees with Holthuis’ (1951)
description in all aspects except with regard to the structure of the second pereopods. The chela of the second right pereopod exhibits an atypical morphology which appears to have resulted from injury. The propodus is abbreviate distally and does not form a normal palm. The dactyl is elongate and overreaches by half its length the tip of the propodus. The distal half of the dactyl is void of teeth. The original second left pereopod has been replaced by a small but normal appearing regenerated appendage.

Remarks.—The two specimens were found in a single specimen of the pen shell *Atrina seminuda* (Lamarck) collected on the beach at South Padre Island. The pen shell bearing the two specimens was just one of many which had been cast ashore by unusually strong onshore winds and currents. Hundreds of specimens of the sea star *Astropecten duplicatus* Gray and sea anemone *Paranthus rapiformis* (Lesueur) were also washed ashore. This is indicative of considerable nearshore bottom disturbance associated with the strong currents which served to both dislodge the above benthic inhabitants and deposit them on the beach.

Distribution.—Although six species of the genus *Pontonia* have been reported from the western Atlantic and eastern Gulf of Mexico (Holthuis 1951; Williams 1965; 1984; Chace 1972), this appears to be the first record of the genus for the Texas coast. The previous westernmost record of *P. domestica* (as *Conchodytes domesticus*) is from the Chandeleur Islands of Louisiana (Cary & Spaulding 1909). This report extends the western range of this species approximately 900 km. The collection locality lies within 15 km of the northeastern coast of Mexico.

*Palaemon floridanus* Chace 1942


Type-locality.—Captiva Island, Lee County on the west coast of Florida.

Material Examined.—Ransom Island, Redfish Bay, Nueces County, Texas, 21 May 1954, coll. H. Hildebrand, three males and 14 females (10 ovigerous) (USNM 96617). South Padre Island, Cameron County, Texas, 15 December 1990, one male and four females (USNM 411882).

Variation.—The largest female specimen from South Padre Island measures 30 mm in total length with a carapace length of 7 mm. The male specimen measures 19 mm in total length with a carapace length
of 4 mm. Both Chace (1942) and Holthuis (1952) noted the close relationship of *Palaemon floridanus* with *Palaemon northropi* (Rankin 1898) which is known to inhabit the "E. American littoral region between Bermuda and Uruguay" (Holthuis 1952:196). Holthuis (1952:169) separated these two species on the basis of the dentition of the ventral margin of the rostrum; *Palaemon northropi* with three or four teeth and *P. floridanus* with five to seven teeth. Specimens from South Padre Island were found to exhibit four to six, usually six, teeth on the ventral margin of the rostrum. As such, the overlap of range of ventral rostral dentition could be used to identify the South Padre Island specimens as belonging to both species. Pending a more comprehensive examination of additional material, the South Padre Island specimens are assigned to *Palaemon floridanus*.

**Remarks.**—*Palaemon floridanus* is found among habitats created by the presence of the artificially constructed rocky revetment protecting the Coast Guard Station on South Padre Island. It lives among rocks extending into the 0.5 to 1 m deep water along the north perimeter. It was also collected from a similar habitat at the eastern abutment of the old and no longer utilized causeway approximately 1 km north of the Coast Guard Station. Specimens are common during the spring and summer months; ovigerous females are present from March to September. Collections are most easily made at night with a light and small dip net.

**Distribution.**—Chace (1942) and Holthuis (1952) report the presence of *Palaemon floridanus* along the west coast of Florida with a single record from the eastern coast. This report is the first record for the Texas coast and extends the western range of this species approximately 1500 km. The collection locality lies within 15 km of the northeastern coast of Mexico.

**Acknowledgments**

This study was supported by a Research Enhancement Grant to the senior author from Angelo State University. The authors wish to thank Elane Stamen for first noting the presence of the *Pontonia* specimens. Appreciation is extended to Dr. Frank Judd and Don Hockaday of the University of Texas-Pan American Coastal Studies Laboratory at South Padre Island. This study would not have been possible without their support.
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Cordylophora lacustris (Cnidaria: Claviidae) from Livingston Reservoir in East Texas

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On 28 January 1995, two specimens of Cordylophora lacustris were recovered from Ekman dredge samples collected from the upper riverine portion of Livingston Reservoir in east Texas. This colonial hydrozoan was first reported in Texas from collections in Angelina, McCulloch, Orange and Pecos counties (McClung et al. 1978). More recent occurrences have been reported in Bosque, Brown, Reeves and Tom Green counties (McClung & Davis 1983). Except for Angelina and Orange counties, previous locality records have been from central and western regions of the state.

Cordylophora lacustris is found in North America in marine waters (Wetzel 1983), brackish inlets and estuaries, and more rarely in inland freshwaters (Pennak 1989). Pennak (1989) reported the occurrence of C. lacustris in rivers of the following states: Tennessee, Oklahoma, Ohio, Illinois, Arkansas, and Louisiana. Additional information relative to anatomy, life cycle, ecology, and biology can be found in Lenhoff & Loomis (1961) and Muscatine & Lenhoff (1974). This report represents the third record of this species from eastern Texas and the first from the Trinity River segment of Livingston Reservoir.

Cordylophora lacustris Allman

Material examined.—Trinity River channel of Livingston Reservoir, 29 km NE of Huntsville, Walker County, Texas, 28 January 1995, two specimens which are deposited with the invertebrate holdings of Stephen F. Austin State University under the direction of Dr. W. W. Gibson.

Habitat.—The collection site on the Trinity River channel is approximately 1 km upstream from the bridge on State Highway 19. Water depth at the site is approximately three meters and the substrate is composed of a thick, mud/clay mixture with limited organic material. One specimen was attached to a small piece of sunken bark and one was free of substrate. Additional collections at two nearby sites failed to produce additional specimens of C. lacustris.

Variation.—The heights of the collected specimens were 27 and 32
mm. This is consistent with Pennak (1989) who reported that this organism in freshwater seldom exceeds 30 mm in height. These specimens are greater in height than those reported by McClung et al. (1978); however, they are not as large as those of *Cordylophora caspia* reported by Poirrer & Denoux (1973), who commonly found specimens as tall as 40 mm. The number of tentacles in the 13 hydranths examined in this study ranged from 7 to 23. According to Pennak (1989), freshwater colonies only produce a few gonophores per colony. McClung et al. (1978) reported that only one gonophore was usually present below a single hydranth, but occasionally two gonophores were present. Poirrer & Denoux (1973) reported the same for freshwater colonies found in Louisiana. The Livingston Reservoir specimens are consistent with the above findings.

**Water chemistry.**—Measurements of temperature, pH, chloride, dissolved oxygen, and total alkalinity from the collection site were within the ranges of those reported by McClung et al. (1978). The specific conductance at the collection site was 110 mhos/cm. This is somewhat below the measurements of 137 to 11,500 mhos/cm previously reported by McClung et al. (1978). Poirrier & Denoux (1973) reported the presence of *Cordylophora caspia* in Louisiana rivers with specific conductance values as low as 72 mhos/cm.

McClung et al. (1978) proposed that increased chloride concentrations tend to produce larger colonies with more tentacles per hydranth in habitats in Texas. Colonies collected from the Pecos River where the chloride concentration was 3,210 mg/L exhibited 7-16 tentacles per hydranth (McClung et al. 1978). This proposal is not in agreement with the present study. The Livingston Reservoir colonies examined during this study were larger, exhibited more tentacles per hydranth (7-23), and were found where the chloride concentration was very low (20.5 mg/L).

Acknowledgments

We wish to thank J.R. Davis, TNRCC, for his consultation and J. Stringer for providing water chemistry data.

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**LASMIGONA COMPLANATA** (BIVALVIA: UNIONIDAE) FROM THE TENSAS RIVER OF NORTHEASTERN LOUISIANA

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During September of 1994, specimens of the white heelsplitter *Lasmigona complanata* (Barnes) were collected from the Tensas River in Madison Parish of northeastern Louisiana. This species was last reported in the state of Louisiana by Vaughn (1893) from Corney Bayou in Union Parish which is located in the northern region of the state.

The bivalve molluscan fauna of the Tensas River, which is a part of the Red River drainage system, was surveyed by Coker (1915), Kuckyr & Vidrine (1975) and summarized by Vidrine (1993). This report adds *Lasmigona complanata* to the 34 species of bivalves reported by Vidrine (1993) as occurring in the Tensas River. It also represents the first published report of this species within the state of Louisiana in more than 100 years. Voucher specimens are deposited with the holdings of the Mississippi Museum of Natural Science (MMNS) in Jackson.
Lasigmonga complanata (Barnes)

Material examined.—Tensas River, 11 km S of Tendal, Madison Parish, Louisiana, 16 September 1994, two specimens (MMNS 3775).

Habitat.—The Tensas River is narrow (6-10 m) at the collection site south of Tendal. Water depth at the time of collection was approximately one meter. Specimens were collected from a substrate consisting of a mixture of sand, gravel and mud. The collection locality lies within the boundaries of the Tensas River National Wildlife Refuge.

Remarks.—Bivalve shells at the collection site were found in association with the silty hornsnail Pleurocera canaliculata (Say). This gastropod was first reported in Louisiana from Bayou Bartholomew in Morehouse Parish by George & Vidrine (1993).

Acknowledgments

This study was done as a part of an investigation of the mussel diversity of the state’s streams conducted during 1994 by the Inland Fisheries Division of the Louisiana Department of Wildlife and Fisheries. We wish to thank Dr. Malcolm F. Vidrine and Steven George for additional field work and Dr. Vidrine for confirming all identifications. The comments and suggestions of Robert G. Howells and an anonymous reviewer were most helpful.

Literature Cited

UTILIZATION OF UNDIGESTED LIVESTOCK FEED GRAIN BY WHITE-WINGED DOVES IN WEST TEXAS

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Zenaida asiatica grandis, one of four subspecies of White-winged Dove found in Texas, occurs naturally in west Texas along the Rio Grande from Presidio northwest to the Sierra Vieja Mountains in southern Presidio County (Saunders 1968). These birds nest and roost along water courses in the area and fly, often great distances, into the mountains and surrounding desert to feed on seeds of native plant species (Cottam & Trefehen 1968). It is presumed that as ranchers settled the area, food, water and cover became available throughout the year and some of the doves have become year round residents.

Feeding dynamics of this and other subspecies of White-winged Doves have only recently been investigated. Engel-Wilson & Ohmart (1978), Gallucci (1978), and Scudday et al. (1980) reported that, when available, seeds of the leatherstem (*Jatropha dioica* Cerv.) are preferred by White-winged Doves, often constituting 100% of crop contents. Leatherstem fruits and seeds are usually present from July through November. Scudday et al. (1980) also noted that during winter months, when seeds from native plants are less abundant, diversity of food items utilized by the White-winged Dove population drops dramatically while diversity within individual bird crops may actually increase. This report, while summarizing the above information, also presents an alternative food source of agricultural origin for the White-winged Dove. This resource is apparently heavily utilized, at least during the cooler times of the year.

For several weeks during March of 1991, over 100 White-winged Doves were observed concentrated near the main ranch house of the Chambers’ Ranch in the Sierra Vieja Mountains. These birds were observed to congregate daily near corrals and stock pens where livestock was being maintained. Despite abundant feed grain available in livestock feed troughs, doves were rarely observed feeding from this potential source of grain. Instead, often in flocks exceeding 50 individuals, the doves consumed undigested corn and other grains from the abundant manure produced by the penned livestock. They were
observed, on occasion, to crowd into an area of the pen in which manure occurred in highest concentrations, appearing to prefer areas where manure had been broken up by the trampling effect of the livestock. The doves were also often observed perching on and picking through intact piles of relatively fresh manure.

This same feeding behavior was also observed during March of 1991 near Mount Ord on the 101 Ranch in central Brewster County. Small flocks of White-winged Doves were noted picking through abundant manure concentrated near several stock tanks and mineral lick sites throughout the northwestern part of the ranch. Although trace amounts of fecal material have been reported from crops of White-winged Doves in Arizona (Haughey 1986), this report, along with a record by Scudday et al. (1980) of what was speculated to be similar behavior, are apparently the first documentation of this type of behavior in White-winged Doves in Texas.

The observations herein reported may in part aid in explaining the relatively recent range expansion as well as population increases of White-winged Doves in this region of west Texas over the past two decades (Small et al. 1989). Along with establishment of suitable nesting habitat, understanding food resources, both natural and supplemental, are crucial to effective management of game species. Consequently, the information provided by these observations may aid in the overall understanding of this species biology and its management requirements.

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HABITAT PARTITIONING BY TWO CONGENERS
(GAMBUSIA GEISERI AND GAMBUSIA NOBILIS)
AT BALMORHEA STATE PARK, TEXAS

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Three species of Gambusia occupy waters in the Pecos River System. Gambusia affinis is widely distributed in eurythermal waters, and G. geiseri and G. nobilis occupy stenothermal spring-fed waters (Hubbs, in press). No prior published report demonstrates habitat segregation between the two stenothermal fishes. Gambusia nobilis is restricted to four spring-associated habitats in Texas and New Mexico and is listed as endangered federally and by both states. Gambusia geiseri is native to the Comal and San Marcos springs and has been introduced into west Texas presumably in the 1930s (Hubbs & Springer 1957). Because the two fishes occupy stenothermal waters, it is possible that the introduced G. geiseri negatively impacts the abundance of the native G. nobilis. The 200 x 4 x 0.5m deep Balmorhea State Park refuge canal was constructed in order to enhance the abundance of G. nobilis and the endangered (U.S. and Texas) Cyprinodon elegans. Seine status surveys have shown that C. elegans abounds in the refuge canal and that G. nobilis is often less abundant than G. geiseri. This study was undertaken to examine the relative abundance of the two species of Gambusia between environments exhibiting different configurations of aquatic vegetation (primarily Chara) by use of dip net samples.
Table 1. Percentage of specimens of *Gambusia* in dip net samples from habitats sampled in the Balmorhea State Park refuge canal.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th><em>Gambusia nobilis</em></th>
<th><em>Gambusia geiseri</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Deep vegetation</td>
<td>74%</td>
<td>26%</td>
</tr>
<tr>
<td>Shallow vegetation</td>
<td>49%</td>
<td>51%</td>
</tr>
<tr>
<td>Over vegetation</td>
<td>7%</td>
<td>93%</td>
</tr>
<tr>
<td>Shallow clear</td>
<td>6%</td>
<td>94%</td>
</tr>
<tr>
<td>Deep clear</td>
<td>12%</td>
<td>88%</td>
</tr>
</tbody>
</table>

The two species were sampled on 9 March 1995 in the Balmorhea State Park refuge canal. A 0.3 x 0.2 m fine-meshed dip net was used. Fish samples were taken from five habitats: in vegetation at the surface, in vegetation at the bottom, in clear surface water over vegetation, in clear surface water, and clear bottom water. The two clear samples had no vegetation within one meter of the sample location. The samples from vegetation had significantly ($\chi^2 p < 0.01$) more specimens of *G. nobilis* than those from open water, regardless of whether there was vegetation below the sample site or no vegetation nearby. The samples from vegetated regions differed in that those from the bottom of the canal had significantly ($p < .01$) more *G. nobilis* than those from the surface. The three open-water samples could not be separated significantly even at the 0.05 level. Nevertheless, those from clear water over vegetation had relatively more specimens of *G. nobilis* than those distant from vegetation, and a higher percentage of *G. nobilis* was from deep water than the similar surface sample, although vastly fewer specimens of *Gambusia* were in the deep sample (primarily *Cyprinodon* were in those samples).

This study concludes that the presence of aquatic vegetation appears beneficial to *G. nobilis* where it is found in sympatric occurrence with *G. geiseri*.

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Texas Academy of Science

March 1 & 2, 1996
Texas A&M University at Galveston

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