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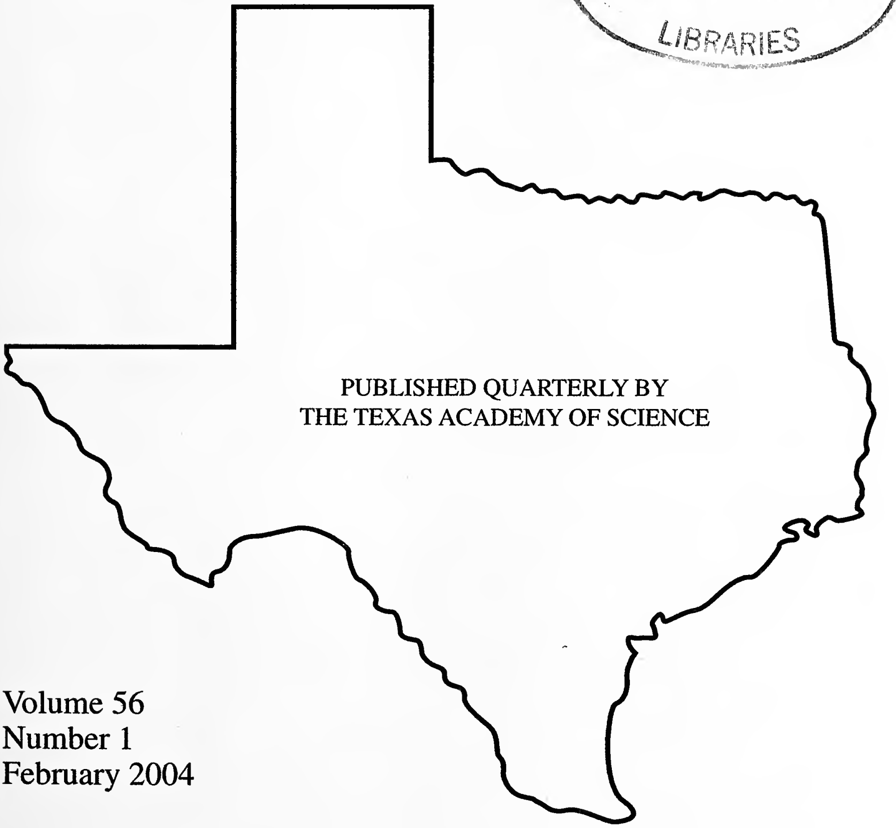

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CONTENTS

GENERAL NOTES

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GROWTH AND SURVIVAL OF *JUNIPERUS ASHEI* (CUPRESSACAE) SEEDLINGS IN THE PRESENCE OF *JUNIPERUS ASHEI* LITTER

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Abstract.—A greenhouse experiment was conducted to determine the effect of *Juniperus ashei* litter on the growth and survival of *J. ashei* seedlings. Incremental additions (0-250 g) of *J. ashei* tree litter or vermiculite (control) were placed on 15 by 15 cm pots, which contained transplanted *J. ashei* seedlings in 800 g of mineral soil. There were no significant differences in the mean absolute differences in growth of *J. ashei* seedling considering basal diameter, seedling height and number of branches between the *J. ashei* tree litter additions and the vermiculite additions, or the amounts of both types of litter. However, there were non-significant positive increases in the seedling growth in the 50 g treatment of both litter types followed by a decrease at higher levels. Mortalities were highest at greater levels of both types of litter, but were still non-significant. The responses of the *J. ashei* seedlings with respect to growth and survival in the *J. ashei* litter and vermiculite suggest that there is no allelopathic component in the *J. ashei* litter affecting seedling growth and survival or if there is, it is transient.

Juniperus ashei is an evergreen, aromatic, dioecious, non-sprouting shrub or small tree (Correll & Johnston 1979). It is usually found on calcareous, rocky, shallow soils from southern Missouri and northern Arkansas through Oklahoma, Texas and parts of northern Mexico (Little 1979; Simpson 1988; Hart & Price 1990; Fuhlendorf et al. 1997). Fourteen species of *Juniperus* have been identified in North America (Little 1979), with over 60 species found worldwide, mostly in semi-arid northern hemisphere ecosystems (Dallimore & Jackson 1967). Various species of *Juniperus* now cover approximately 10 million hectares in Texas (Gould 1969). *Juniperus ashei* is a dominant species of many savannahs and woodlands of the Edwards Plateau of central Texas (Van Auken et al. 1980). Estimated density of *J. ashei* in central Texas ranges from approximately 700 trees ha^{-1} to 1500 trees ha^{-1} (Van Auken et al. 1979; Smeins 1990).

Evidence suggests that *J. ashei*, as well as some other species of

Juniperus, have increased in density since European settlement by encroachment into adjacent grasslands (Buechner 1944; Smeins 1980; Fuhlendorf et al. 1996; Van Auken 2000). Historically, *J. ashei* was apparently restricted to canyons, rocky outcrops or areas with shallow soils, which were protected from grassland fires (Ellis & Schuster 1968). The most widely cited explanation for woody plant encroachment attributes the shifts in community types to a concomitant reduction in fire frequency and decreased competition from grasses, both of which are promoted by heavy grazing by domestic ungulates (Neilson 1986; Archer et al. 1988; Schlesinger et al. 1990; Bashre 1991; Van Auken 2000).

There are many reports of allelopathic effects of litter or litter extracts on various understory species, including woody plant seedlings (Rice 1984). Suppression of understory vegetation by *J. osteosperma* is commonly reported in New Mexico and Arizona (Arnold et al. 1964) and *J. virginiana* and *J. pinchott* may reduce herbaceous cover and diversity (Arnold et al. 1964; Engle et al. 1987; Armentrout & Pieper 1988). *Juniperus monosperma* litter seems to have a negative effect on the growth of *Bouteloua gracilis* (blue grama) (Jameson 1966; Jameson 1970b). In addition, reduction of herbaceous vegetation has been reported below *Juniperus* canopies even after canopy removal (Bonnett 1960; Jameson 1966; Jameson 1970b; Carson 1990; Barnes & Archer 1996). However, the cause of the apparent allelopathic effects is unclear.

Juniperus ashei has been observed with a zone of reduced herbaceous cover and diversity beneath the crown near the stem (Blomquist 1990; Fuhlendorf 1992). In closed-canopy stands, *J. ashei* like other *Juniperus* sp. can exclude most herbaceous vegetation (Buechner 1944; Johnsen 1962; Burkhart & Tisdale 1969; Yager & Smiens 1999). However, there are some places below the canopy that *Carex planostachys* (cedar sedge) has high cover (Wayne 2000; Wayne & Van Auken 2002). *Juniperus ashei* tree litter was demonstrated to have negative effects on seedling recruitment and germination of some herbaceous species including grasses, but negative effects were reduced or absent on a woody plant seedling (*Sophora secundiflora*) by Yager & Smeins (1999). In addition, litter apparently reduced the density of most woody and herbaceous species even after adult *J. ashei* canopies were completely removed (Yager & Smeins 1999). However, *J. ashei* seedlings have been observed to rapidly establish following the removal of the adult canopy (Weniger 1984; Owens 1995).

Juniperus ashei seedlings below the adult canopy in woodlands have a lower mortality and lower growth rates than seedlings near the canopy edge adjacent to grasslands or gaps (Jackson & Van Auken 1997). *Juniperus ashei* seedlings in these woodlands decreased exponentially through time with 1-18% surviving eight years, depending on the cohort. Gradients of light levels, soil moisture, organic content and surface temperatures occur from under the adult *J. ashei* canopy into the adjacent grasslands or gaps (Wayne 2000; Wayne & Van Auken 2002). It seems clear that adult *J. ashei* trees have a direct or indirect influence on the growth and survival of *J. ashei* seedlings. Part of this influence may be caused by the presence of *J. ashei* tree litter.

Tree litter has been shown to have a mixed influence on the growth and development of canopy tree seedlings. Negative influences may include shading, crushing, allelopathy, limiting water absorption and isolation of the seedling roots from the mineral soil (Johnsen 1962; Bergelson 1990; Bosy & Reader 1995; Milton 1995; Yager & Smiens 1999). There are also some positive influences that have been associated with tree litter, including reduction in competition from herbaceous species, protection from desiccation, increased soil aeration and nutrient release from litter decomposition (Fowler 1986; Facelli & Pickett 1991; Facelli 1994; Yager & Smiens 1999). The purpose of this study was to examine the potential effects of *J. ashei* tree litter on the growth and survival of *J. ashei* seedlings.

MATERIALS AND METHODS

This study was conducted for five months from 15 June 2001 to 15 November 2001 at the University of Texas at San Antonio in a forced air, temperature controlled (21-29°C) fiberglass greenhouse. Light levels for photosynthetically active radiation (PAR, λ = 400 to 700 nm) were ≈ 400 μmole m^{-2} s^{-1} inside the greenhouse and under 50% shade cloth on a cloudless day at solar noon on 7 September 2001 (22% of outdoor ambient light), which approximated light levels under intact *J. ashei* canopies. Light levels were measured with a LI-COR® LI-190SA integrating quantum sensor and recorded using a LI-COR® LI-1000 Data Logger using a 60 s average (5 s intervals).

Juniperus ashei tree litter was collected in Eisenhower Park (29°37'19"N, 98°34'26"W, 322 m height above ellipsoid, in northern

Bexar County) on 1 May 2001 from under ten *J. ashei* trees. At each *J. ashei* tree, five 0.1 m^2 sites with tree litter present were arbitrarily chosen. The tree litter (O-horizon) was comprised mainly of debris in various stages of decomposition (fresh to highly decomposed) from the adult *J. ashei* trees, which included leaves, cones, bark, small branches and seeds. Five approximately equal samples from under each sampled tree were collected to a maximum depth of approximately 10 cm with a hand trowel and placed in a large plastic trash bag. The cumulative sample from all ten *J. ashei* trees was mixed thoroughly by hand and spread out on the cement greenhouse floor and air-dried for 14 d. Schultz® Horticultural Vermiculite was used as a control to simulate the physical, but not chemical properties of *J. ashei* litter. The vermiculite was washed thoroughly with approximately 15 liters of deionized water in 25 liters containers. The excess water was then poured off and the remaining vermiculite was spread out and air-dried on the greenhouse floor in a comparable fashion as the *J. ashei* litter.

Recently emerged *J. ashei* seedlings (only cotyledons present) were transplanted from Eisenhower Park, into 15 by 15 cm plastic pots lined with Ziploc® bags to prevent water and nutrient loss (n = 72). Each pot was filled with 800 g of sieved (4 mm mesh), air-dried, low nutrient, non-fertilized, clayey over sandy or sandy skeletal, carbonatic, thermic Typic Calciustoll (United States Department of Agriculture, 2000) in the Patrick association, obtained in northern Bexar County. Fertilizer was not added because the growth of *J. ashei* seedlings did not appear to be limited (having substantial growth) in prior experiments, which used the same soil and approximately the same mass. On 15 May 2001 pots were randomly assigned treatments that consisted of adding different levels of *J. ashei* tree litter or vermiculite. Treatments of 0, 50, 100, 150, 200 and 250 g (n = 6 for each level) of either washed, air dried vermiculite or air dried *J. ashei* tree litter were placed on top of the mineral soil with care given to prevent the burial of the *J. ashei* seedlings. All pots were initially watered with 300 mL of deionized water after transplantation. Seedling treatments were initially randomized on greenhouse tables for treatment and replicate, and to minimize edge effects were rearranged randomly every 2 wk. The pots were watered as needed with 50-150 mL of deionized water (every 4-8 days). Seedlings were allowed 30 d from the initial transplantation to recover from any transplant shock. During the transplant recovery period (15 May – 15 June) 13 seedlings died, and were not considered in the study. Thus, total n = 59 and sample size per treatment were unequal.

Basal diameter, height and number of branches were measured for each *J. ashei* seedling at the beginning of the experiment (15 June 2001) and at the termination of the experiment (11 November 2001). A 1 mm dot of nail polish was used to mark all *J. ashei* seedlings on the main stem 3 cm from the top of the mineral soil. All basal diameter measurements were made immediately above this mark using a digital caliper (Mitutoyo®, model CD-6"P). Each basal diameter measurement, measured in millimeters, was a mean of six measurements; the first three were taken from the north to south facing direction of the seedling and the last three at the east and west facing direction of the *J. ashei* seedling. *Juniperus ashei* seedling height, measured in centimeters, was measured from the nail polish mark to the top of the leaves on the uppermost living branch of the seedling. The number of branches for each *J. ashei* seedling was determined by counting all living branches greater than 2 mm in length. When branches or entire seedlings were presumed to have died (green tissue was no longer visible) response variables were not measured, and a zero was recorded for its measurement.

Absolute differences in growth (final measurement minus initial measurement) for basal diameter, height and number of branches were analyzed with a two-way *ANOVA* with interaction to determine significant differences between litter types (2 levels) and amounts (6 levels). Also, numbers of seedling mortalities were analyzed between the litter treatment types and amounts with chi-squared analysis. Expected values for the chi-squared analysis were adjusted to account for unequal initial sample size by multyplying cumulative mean percent mortality by the initial sample size.

RESULTS

The overall models for the two-way *ANOVA's* of the absolute differences in growth of the three response variables were not significant (basal diameter $F = 1.41$, $P = 0.20$, basal diameter $F = 1.43$, $P = 0.19$, basal diameter $F = 1.00$, $P = 0.46$), which indicated that there were no significant differences between litter types and amounts, or the two-way interaction.

Generally, seedlings in the vermiculite treatment had greater absolute differences in growth for height, branches, and basal diameter than their *J. ashei* litter counterparts (24% for height and 3% for number of seedling branches and 13% for basal diameter), but again none of these

Table 1. Sample size, absolute final mean (± *SD*) growth difference (final minus initial measurements), in the *J. ashei* litter and vermiculite treatments. Although there is a decrease in the response variables with increased litter inputs, there are no significant differences between any of the response variables with litter types or amounts (two-way *ANOVA's*). Some measures of variance (*SD*) are not reported (na), due to small or missing samples.

Sample (*n*)		Basal diameter (mm)		Height (cm)		# of Branches	
Litter amount	J/V litter	*J. ashei* litter	Vermiculite	*J. ashei* litter	Vermiculite	*J. ashei* litter	Vermiculite
0	6/4	0.00 ± 0.14	0.07 ± 0.05	2.68 ± 1.81	4.61 ± 1.29	3.0 ± 2.6	2.0 ± na
50	6/6	0.14 ± 0.15	0.35 ± 0.29	2.40 ± 0.58	2.78 ± 1.58	4.6 ± 2.1	4.0 ± 3.6
100	6/5	0.20 ± 0.25	0.21 ± 0.04	2.83 ± 2.99	1.00 ± 0.85	4.5 ± 6.4	3.5 ± 0.7
150	4/5	0.11 ± 0.24	0.03 ± na	1.73 ± 0.59	3.20 ± na	3.0 ± 3.0	9.0 ± na
200	4/5	0.05 ± 0.05	0.00 ± na	1.65 ± 0.78	0.00 ± na	1.0 ± 1.4	0.0 ± na
250	5/3	0.00 ± na	0.00 ± na	0.00 ± na	0.00 ± na	0.0 ± na	0.0 ± na

differences were significant (Table 1). Fifty g of *J. ashei* litter and vermiculite had the greatest increase in mean absolute differences for basal diameter (86%) and number of branches (42%), alternately mean absolute differences for height decreased (41% less) compared to no litter and no vermiculite treatments. Mean absolute differences generally decreased with increased amounts of both litter types over 50 g, until 100% mortality occurred in the 200 g and 250 g of vermiculite and in 250 g of *J. ashei* litter. Standard deviations were large, being equal to the treatment mean in many cases (Table 1).

Seedling mortalities were analyzed between the litter treatment types and amounts to determine if a particular treatment or treatments induced greater mortality. There were no significant differences in mortality between vermiculite (19) and *J. ashei* (13) litter ($X^2 = 2.01$, $P = 0.16$, *df* 1) (Table 2). Although mortality in both treatments increased with increased amounts of *J. ashei* litter or vermiculite (ranging from 25-100%), there were also no significant differences in mortality with respect to litter amounts of both treatments combined ($X^2 = 6.46$, $P = 0.26$, *df* 5).

DISCUSSION

An allelopathic effect claimed for litter of some species of *Juniperus* (Jameson 1970a; Jameson 1970b; Whittaker & Feeney 1971; Everett et al. 1983; Rice 1984) and for the litter of many other species (Rice 1984) was not demonstrated in the present study. Allelopathic substances, if present, may be transitory due to rapid decomposition of possible growth

Table 2. Seedling mortalities in the *J. ashei* litter and vermiculite treatments, including number of mortalities for both types and amount of litter. The initial sample size *n* is given in parenthesis. There were no significant differences in mortality between the litter types (X^2 = 2.01, *P* = 0.16, *df* 1). There were also no significant differences in mortality with respect to litter amounts of both treatments combined (X^2 = 6.46, *P* = 0.26, *df* 5).

Litter Amount (g)	% Mortality Tree Litter	 Vermiculite	 Mean
0 (10)	33% (6)	50% (4)	40%
50 (12)	17% (6)	33% (6)	25%
100 (11)	33% (6)	60% (5)	45%
150 (9)	25% (4)	80% (5)	55%
200 (9)	50% (4)	100% (5)	78%
250 (8)	100% (5)	100% (3)	100%
Mean	42% (*n*=31)	68% (*n*=28)	54% (*n*=59)

inhibitors in the litter (Jameson 1970a) or leaching from the system (Rice 1984). The effects observed in the present study appear to be caused by physical effects independent of the litter type used. The effects of these organic (*J. ashei* litter) and inorganic (vermiculite) substances in terms of absolute differences in growth and mortalities appear not only to be statistically homologous between treatment type, but also the trends appear to be similar across treatment amounts. These patterns strongly suggest that an allelopathic component in the *J. ashei* litter was not present and consequently had little or no influence on the growth of the *J. ashei* seedlings.

Differences in mortality between the *J. ashei* tree litter and vermiculite (control) treatments overall (Table 2) indicate that the seedling mortality was lower in the *J. ashei* litter treatment (42%) compared to the vermiculite treatment (68%), but very high mortality (100%) was found in the *J. ashei* litter and also in the vermiculite. An organic component cannot be ruled out as positively influencing *J. ashei* seedling mortality, because of observed decreases in seedling mortality in the lower *J. ashei* litter treatments. However, the same trend was found in the vermiculite treatment.

Some positive effects of litter in field situations have been cited, which are conservation of water during dry conditions (Fowler 1986) and adding nutrients to the soil after litter decomposition (Facelli &

Pickett 1991). Nutrients released from the *J. ashei* litter or moisture loss prevention properties of the litter are not plausible explanations for the observed changes in growth and mortality in the present study. Vermiculite is thought to have provided little or no nutrients to the soil during the experimental period. Consequently, the positive effects on seedling growth seen by both litter types at low addition levels were not likely a nutrient effect. The hydrophobic effects that litter may have (Gifford 1970; Yager & Smiens 1999), which could limit, or conversely improve water availability for the seedlings in field settings were not tested in the current study, because the study attempted to reduce unwanted variability by keeping the soil moist at all times. Furthermore, the observed effects cannot be attributed to prevention of the seedling roots reaching the mineral soil since the seedlings in this study were initially planted in mineral soil.

The small increase in the mean absolute growth differences and decreased mortality (25% compared to the mean of 54% for all seedling treatments) of the seedlings in the 50 g litter treatments (cumulative for *J. ashei* and vermiculite litter) in the present study may have been caused by soil aeration. Aeration by plant litter has been shown to occur, and it is important in rooting depth, root respiration and even nitrogen fixation in some plants (Khan et al. 2000). Greater aeration could have been caused inadvertently in the present study by small amounts of mixing of the upper soil layers in both litter types during the initial setup.

Indirect influence of the litter on other organisms closely associated with the *J. ashei* seedlings in the field should also be considered. *Juniperus ashei* tree litter or vermiculite may facilitate a favorable microenvironment (temperature and moisture), benefiting soil animals, fungi or microorganisms (Sylvia et al. 1998). The favorable microclimate may facilitate nitrogen mineralization, increasing inorganic nitrogen availability, which is a primary limiting nutrient in most North American terrestrial ecosystems. Also, existing relationships that *J. ashei* seedlings may have with various organisms may also depend on the presence of *J. ashei* litter for a labile carbon source, ultimately enhancing nitrogen availability.

The effects of litter may be difficult to demonstrate in field settings, because the presence of litter may alter resource availability so that litter suppression and resource competition are interlinked, and therefore confounding (Foster & Gross 1997; Foster & Gross 1998). Jackson & Van Auken (1997) found that seedling mortality was lowest under intact canopies, which have substantial amounts of *J. ashei* litter. Findings from this current study corroborate this previous observation, that *J. ashei* litter apparently does not interfere with *J. ashei* seedling growth and potentially may even enhance growth and lower mortality for seedlings growing in shallow O-horizons. In a field setting, reduction of herbaceous vegetation including grass species in *J. ashei* woodlands might be important for the initial establishment of the *J. ashei* seedlings, possibly until both the roots of the *J. ashei* seedlings are beyond depth of root competition and aboveground competition for light is reduced. A possible mechanism of intraspecific seedling facilitation by the adult *J. ashei* trees and specifically *J. ashei* litter may be the reduction in competition from herbaceous and other woody species, in addition to an improvement in seedling growth and mortality caused by the physical presence of underlying litter. However, large amounts of *J. ashei* litter may reduce the growth and survival of the *J. ashei* seedlings, as well as competing species, forfeiting any potential advantage the presence of the litter may provide for *J. ashei* seedlings. *Juniperus ashei* litter may play an important part in *J. ashei* seedling establishment, ultimately affecting the replacement and population dynamics of this species, but this role appears difficult to detect.

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THE VASCULAR FLORA OF THE PALO ALTO NATIONAL BATTLEFIELD HISTORIC SITE, CAMERON COUNTY, TEXAS

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Abstract.—A checklist is provided of the vascular plant taxa of the 1,376 ha Palo Alto Battlefield National Historic Site (PABNHS) in Cameron County of south Texas. PABNHS consists of four plant communities: resacas and tanks, salt flats, brush-grasslands and coastal marshes. Vascular plants of disturbed sites are noted. Two hundred forty-three taxa in 66 families are documented and their community affiliations are given. Three families, Poaceae, Asteraceae and Fabaceae contain 37.5% of the species richness at PABNHS.

The southernmost extension of prairie in the United States is located in the Gulf Prairies and Marshes vegetation area of Texas (Schuster & Hatch 1990). Saline sites in the prairie in southern Texas that are flooded intermittently are usually dominated by *Spartina spartinae* (gulf cordgrass), often to the exclusion of other species (Oefinger & Scifres 1977; Scifres et al. 1980; Smiens et al. 1991). Küchler (1964) combined upland *Andropogon/Schizachyrium* and/or *Bothriochloa* prairies with *S. spartinae* marshes and referred to the entity as a Southern Cordgrass Prairie, and Diamond et al. (1987) referred to this community as a Gulf Cordgrass Series. Turner (1959), the only investigator using quantitative methods, mapped most of south Texas in the Tamaulipan ecoregion (MacRoberts & MacRoberts 2003).

Johnston (1955; 1963) stated that the poorly drained flats near the coast in Cameron County support a salt prairie. He reported that the area is dominated by halophytic subshrubs including *Batis maritima, Salicornia virginica, Suaeda* sp., *Borrichia frutescens* and the mat-forming grass, *Monanthochloë littoralis*. Low-lying saline, sometimes water-logged clays at elevations from 0 m to 3 m above sea level are referred to as "Borrichia flats" (Johnston 1955; 1963). Lonard et al. (1991) partitioned the natural vegetation of the lower Rio Grande Valley into four major habitats (1) Rio Grande floodplain, (2) coastal prairies and marshes, (3) barrier islands and (4) brush-grasslands, and they provided brief descriptions of these habitats.

The U.S. National Park Service proposes to restore the battlefield landscape at the Palo Alto National Battlefield National Historic Site (PANBHS) to the putative conditions at the time of the first battle of the Mexican-American War (1846-1848). U. S. Grant noted in his war diary that the grass (*S. spartinae*) that dominated the wet battlefield ... "was tall, reaching the shoulders of the men, very stiff, and each stock pointed at the tip, and hard, almost as sharp as a darning needle" (Sanchez 1985). The restoration will include the highly disturbed core battlefield site in the coastal marsh formerly dominated by gulf cordgrass and the adjacent resaca (remnant shallow, abandoned river channel of the historic floodplain of the lower Rio Grande) that provided water for the combatants.

Little is known about the extant vascular plant species richness of this National Historic Site. Only one unpublished checklist of vascular plants is available (Richard & Richardson 1993) for the site. Thus there has been no comprehensive study of the flora of PANBHS. The purpose of this paper is to identify the vascular flora of this segment of the Rio Grande Delta.

STUDY SITE

A broad delta has been formed by the Rio Grande on the Texas mainland where the river approaches the Gulf of Mexico. The delta fronts the coastline from 25° 30' to 26° 30' N latitude between Port Mansfield in Willacy County and the mouth of the Rio Grande in Cameron County. At least three major Holocene lobes were formed by the Rio Grande fluvial-deltaic system (Brown et al. 1980). The study site, characterized by numerous resacas, is located in the Del Tigre intermediate sub-delta where the river shifted into Mexico. The northwestern extension of the delta is 67 km upstream from the Gulf of Mexico and includes all of Cameron County (Clover 1937; Brown et al. 1980; Judd & Lonard 2002).

PANBHS about 16.1 km north of the Rio Grande is located at the intersection of two roads, F.M. 511 and F.M. 1487, in Cameron County, Texas. The 1,376 ha National Park Unit is in a broad, undeveloped prairie interspersed with stands of mixed brush and several lengthy resacas. The area is in the Matamoros district of the Tamaulipan Biotic Province (Blair 1950).

All soils at PANBHS are saline clays or clay loams (Table 1) (Williams et al. 1977). The highly saline Lomalta Clay is the predominant soil series. It includes the substrate of the core battlefield site and

Table 1. Soil series and vegetation zones at Palo Alto National Battlefield Historic Site. RT = resacas and tanks, SF = salt flats, CM = coastal marshes and BG = brush-grasslands.

Soil Series	Percent of Area	Vegetation Zones
Lomalta clay	62.6	RT, SF, CM
Chargo silty clay	12.9	BG
Laredo silty clay loam, saline	8.4	RT margins, SF, CM
Laredo silty clay loam	6.0	BG
Sejita silty clay loam	5.0	CM, SF
Latina sandy clay	2.9	SF, CM
Benito clay	2.2	CM, SF

resaca systems. Vegetation zones that occur here are coastal marshes (*S. spartinae* community), salt flats and resacas and tanks. The less saline Chargo Silty Clay and Laredo Silty Clay Loam Series (18.9%) of the area occur at elevations greater than 4.6 m above sea level and support brush-grassland vegetation (Table 1). The topography is flat, and the elevation is 2.96 m to 6.37 m above sea level. The water table typically ranges from 45 to 91 cm below the soil surface (Williams et al. 1977).

The climate of the area is semi-arid (Thornthwaite 1948) with an annual precipitation of about 66 cm (Lonard et al. 1991). Rainfall peaks are in September and October. The mean frost free period is 330 days, and frequently an entire winter will pass without freezing temperatures (Lonard et al. 1991).

Although the site retains some of its original integrity, most of PANBHS has been disturbed. Resaca channels have been excavated or blocked to form small tanks. Grazing, farming, road building and excavation of drainage canals have altered landscape features. Abandoned cultivated fields, established in the 1940's, occupy the core battlefield area, and secondary succession has not resulted in the return of a *S. spartinae* community.

METHODS

Data reported here are based primarily on collections made by Richardson and Richard in 1992 and 1993 and by Richardson in 1991.

Table 2. Summary of the vascular flora of Palo Alto Battlefield National Historic Site, Cameron County, Texas.

	Polypodiopsida	Magnoliopsida	Liliopsida	Total
Families	1	54	11	66
Genera	1	148	39	188
Species	1	182	60	243
Native species	1	170	52	223
Introduced species	0	12	8	20

Lonard conducted monthly surveys between June and November 2001 and from December 2002 to June 2003. Vouchers were deposited in the University of Texas-Pan American Herbarium (PAUH). Nomenclature including common names follows Jones & Wipff (2003). Abbreviations are used to refer to vegetation zones or sites recognized in Lonard et al. (1991). A category, disturbed sites, has been added to include areas altered by farming, grazing, or road construction. Abbreviations and vegetation zones and sites are:

RT – Resacas and tanks

SF – Salt flats

CM – Coastal marshes

BG – Brush-grasslands

DS – Disturbed sites

I - Introduced

RESULTS AND DISCUSSION

This study reports the presence of 243 species of vascular plants representing 188 genera and 66 families from PANBHS (Table 2). The three most common families are Poaceae (16.5%), Asteraceae (15.2%) and Fabaceae (5.8%). Thirty families are represented by a single species, and 20 species have been introduced.

CHECKLIST OF THE VASCULAR FLORA OF THE PALO ALTO NATIONAL HISTORIC SITE, CAMERON COUNTY, TEXAS

POLYPODIOPSIDA (FERNS)

MARSILEACEAE

Marsilea macropoda (G. Engelmann *ex* A. Braun) A. Gray. Water-clover, (RT).

MAGNOLIOPSIDA (DICOTS)

ACANTHACEAE

Dyschoriste crenulata C. Kobuski. Crenate-leaf snake-herb, (BG).

Elytraria bromoides A. Oersted. Wheat-spike scaly-stem, (BG).

Justicia pilosella (C. Nees von Esenbeck) R. Hilsenbeck. Tube-tongue, (BG).

Ruellia nudiflora (G. Engelmann *ex* A. Gray) I. Urban var. *runyonii* (B. Tharp & F. Barkley) B.L. Turner. Runyon's violet wild-petunia, (BG).

Stenandrium dulce (A. Cavanilles) C. Nees von Esenbeck. Sweet shaggy-tuft, (BG).

ACHATOCARPACEAE

Phaulothamnus spinescens A. Gray. Snake-eyes, (BG).

AIZOACEAE

Sesuvium verrucosum C. Rafinesque-Schmaltz. Winged sea-purslane, (RT, DS, SF).

Trianthema portulacastrum C. Linnaeus. Desert horse purslane, (DS).

AMARANTHACEAE

Alternanthera paronychioides A. de Saint-Hilaire. Smooth joy weed, (RT).

Amaranthus blitoides S. Watson. Prostrate pigweed, (DS, I).

Celosia nitida M. H. Vahl. West Indian cock's-comb, albahaca, (BG).

APIACEAE

Cyclospermum leptophyllum (C. Persoon) T.A. Sprague *ex* N. Britton & Percy Wilson. Slim-lobe celery, (DS, I).

Eryngium nasturtiifolium A.L. de Jussieu *ex* F. Delaroche. Hierba del sapo, (RT, DS).

ASCLEPIADACEAE

Cynanchyum barbigerum (G. Scheele) L. Shinners. Swallow-wort, (BG, DS).

ASTERACEAE (Compositae)

Acourtia runcinata (M. Lagasca y Segura *ex* D. Don) B.L. Turner. Stemless desert peonia, (BG).

Aphanostephus ramosissimus A. P. de Candolle. Plains lazy-daisy, (DS).

Ambrosia psilostachya A. P. de Candolle. Western ragweed, (DS).

Baccharis neglecta N. Britton. Roosevelt weed, (DS).

Bidens laevis (C. Linnaeus) N. Britton, E. Sterns & J. Poggenbery. Smooth beggar-ticks, (RT).

Borrichia frutescens (C. Linnaeus) A.P. de Candolle. Sea-ox-eye daisy, (RT, SF, CM, DS).

Calyptocarpus vialis C. Lessing. Straggler daisy, (DS).

Chromolaena odorata (C. Linnaeus) R. King & B. Robinson. Crucita, (BG, DS).

Cirsium texanum S. Buckley. Southern thistle, (DS).

Clappia suaedifolia A. Gray, Fleshy-leaf clappia, (SF, DS).

Coreopsis tinctoria T. Nuttall. Golden wave, (RT, DS).

Dyssodia pentachaeta (A.P. de Candolle) B. Robinson. Parralena, (BG, DS).

Dyssodia tenuiloba (A.P. de Candolle) B. Robinson var. *treculii* (A.Gray) J. Strother. Bristleleaf dyssodia, (BG, DS).

Eclipta prostrata (C. Linnaeus) C. Linnaeus. Yerba de tago, (RT).

Erigeron tenellus A.P. de Candolle. Fleabane, (DS).

Evax verna C. Rafinesque-Schmaltz. Spring evax, (DS).

Fleishmannia incarnata (T. Walter) R. King & H. Robinson. Flesh-pink fleishmannia, (BG, DS).

Florestina tripteris A. P. de Candolle. Three-lobed florestina, (DS).

Gamochaeta falcata (J. de Lamarck) A. Cabrera. Sickle cudweed, (DS, I).

Gamochaeta pensilvanica (C. von Wildenow) A. Cabrera. Purple

cudweed, (DS).
Gutierrezia texana (A. P. de Candolle) J. Torrey & A. Gray. Texas snakeweed, (DS).
Helenium microcephalum A.P. de Candolle var. *oöclinum* (A. Gray) M. Bierner. Sneeze-weed, (RT).
Helianthus annuus C. Linnaeus. Sunflower, (DS).
Isocoma drummondii (J. Torrey & A. Gray) Greene. Drummond's jimmyweed, (BG, DS).
Machaeranthera phyllocephala (A. P. de Candolle) L. Shinners. Camphor tansy-aster, (SF, DS).
Packera tampicana (A. P. de Candolle) C. Jeffrey. Tampico butterweed, (RT, DS).
Parthenium hysterophorus C. Linnaeus. Ragweed parthenium, false ragweed, (DS).
Pluchea purpurascens (O. Swartz) A. P. de Candolle. Purple marsh-fleabane, (RT).
Senecio ampullaceus W. Hooker. Groundsel, (BG, Texas endemic).
Simsia calva (G. Engelmann & A. Gray) A. Gray. Bush sunflower, (BG).
Sonchus asper (C. Linnaeus) J. Hill. Rough sow thistle, (DS, I).
Sonchus oleraceus C. Linnaeus. Common sow thistle, (DS, I).
Symphyotrichum divaricatum (T. Nuttall) G. Nesom. Wireweed, salt-marsh aster, (DS, RT).
Trichocoronis wrightii (J. Torrey & A. Gray) A. Gray. Wright's bugheal, (RT, CM).
Verbesina encelioides (A. Cavanilles) G. Bentham & J. Hooker *ex* A. Gray. Cowpen daisy, (DS).
Verbesina microptera A.P. de Candolle. Capitana crownbeard, (BG, DS).
Wedelia texana (A. Gray) B. L. Turner. Texas wedelia, (BG).

BATACEAE
Batis maritima C. Linnaeus. Maritime saltwort, vidrillos, (RT, SF, CM).

BORAGINACEAE
Heliotropium angiospermum J. Murray. Taper-leaf heliotrope, (DS, RT).
Heliotropium curassavicum C. Linnaeus. Seaside heliotrope, (RT, SF, CM, DS).

BRASSICACEAE

Lepidium austrinum J. K. Small. Southern pepperwort, (DS).

Lepidium lasiocarpum T. Nuttall *ex* J. Torrey & A. Gray var. *wrightii* (A. Gray) C. Hitchcock. Wright's woolly-fruit pepperwort, (DS).

Lesquerella argyraea (A. Gray) S. Watson. Narrow-leaf bladderpod, (DS).

Lesquerella lasiocarpa (W. Hooker *ex* A. Gray) S. Watson var. *berlandieri* (A. Gray) E. Payson. Berlandier's woolly-pod bladderpod, (DS).

Sisymbrium irio C. Linnaeus. London rocket, (DS, I).

CACTACEAE

Acanthocereus tetragonus (C. Linnaeus) E. Hummel. Barb-wire cereus, (BG).

Cylindroopuntia leptocaulis (A.P. de Candolle) K. Kunth. Tasajillo, desert Christmas cactus, (BG, DS).

Echinocactus texensis C. Höpffer. Devil's head, (BG).

Echinocereus pentalophus (A. P. de Candolle) C. Lemaire. Lady-finger hedge-hog cactus, (BG).

Mammillaria heyderi F. Mühlenpfordt. Heyder's pinchusion cactus, (BG).

Opuntia engelmannii J. Salm-Reifferscheid-Dyck. Engelmann's prickly pear, (BG, DS).

Telocactus setispinus (G. Engelmann) E. Anderson. Miniature barrel cactus, (BG).

CAMPANULACEAE

Lobelia berlandieri A. L. de Candolle. Lobelia, (DS).

CAPPARACEAE

Koeberlinia spinosa J. Zuccarini. Allthorn, crucifixion-thorn, (BG).

CELASTRACEAE

Maytenus phyllanthoides G. Bentham. Mangle-dulce, (BG, SF, DS).

Schaefferia cuneifolia A. Gray. Desert yaupon, (BG).

CHENOPODIACEAE

Atriplex matamorensis A. Nelson. Matamoros saltbush, (SF, DS).

Atriplex pentandra (N. von Jacquin) P. Standley. Quelite saltbush, (SF, DS).

Chenopodium berlandieri C. Moquin-Tandon. Goosefoot, (DS).
Chenopodium murale C. Linnaeus. Nettle-leaf goosefoot, (DS, I).
Salicornia virginica C. Linnaeus. Perennial saltwort, (SF).
Suaeda linearis (S. Elliott) C. Moquin-Tandon. Annual seepweed, (SF, DS).
Suaeda tampicensis (P. Standley) P. Standley. Tampico seepweed, (SF, DS).

CLUSIACEAE
Hypericum pauciflorum K. Kunth. Few-flowered St. John's wort, (BG, DS).

CONVOLVULACEAE
Dichondra micrantha I. Urban. Small-flowered pony foot, (BG, DS).
Evolvulus alsinoides (C. Linnaeus) C. Linnaeus var. *angustifolius* J. Torrey. Ojo de víbora, (BG, DS).
Evolvulus sericeus O. Swartz. Silky dwarf morning glory, (DS).

CRASSULACEAE
Kalanchoë delagoënsis C. Ecklon & C. Zeyher. Kalanchoe, (DS, I).
Lenophyllum texanum (J. G. Smith) J. Rose. Texas stonecrop, (BG).

CUCURBITACEAE
Ibervillea lindheimeri (A. Gray) E. Greene. Lindheimer's globeberry, (BG, DS).
Melothria pendula C. Linnaeus. Drooping melonette, (DS).

EUPHORBIACEAE
Chamaesyce serpens (K. Kunth) J.K. Small. Matted sand-mat, (DS).
Croton capitatus A. Michaux var. *lindheimeri* (G. Engelmann & A. Gray) J. Müller of Aargau. Lindheimer's hogwort croton, (DS).
Croton leucophyllus J. Müller of Aargau. Croton, (DS).
Ditaxis humilus (G. Engelmann & A. Gray) F. Pax. Low-growing silverbush, (DS).
Jatropha cathartica M. Terán & J. Berlandier. Geranium-flowered jatropha, (BG).
Jatropha dioica M. Sessé y Lacasta *ex* V. de Cervantes. Leather-stem, (BG).
Phyllanthus polygonoides T. Nuttall *ex* K. Sprengel. Knot weed leaf flower, (DS).

FABACEAE (Leguminosae)

Acacia farnesiana (C. Linnaeus) C. von Willdenow. Huisache, (CM, RT, DS).

Chloroleucon ebano (J. Berlandier) L. Rico. Texas ebany, (BG).

Dalea pogonothera A. Gray var. *walkerae* (B. Tharp & T. Barkley) B.L. Turner. Bearded dalea, (DS).

Dalea scandens (P. Miller) R. Clausen var. *paucifolia* (J. Coulter) R. Barneby. Low dalea, (BG).

Desmanthus virgatus (C. Linnaeus) C. von Willdenow var. *depressus* (F. von Humboldt & A. Bonpland) *ex* C. von Willdenow) B. L. Turner. Bundleflower, (DS).

Leucaena pulverulenta (D. von Schlechtendal) G. Bentham. Tepeguaje, (BG).

Melilotus albus F. Medikus. White sweetclover, (DS, I).

Mimosa asperata C. Linnaeus. Black mimosa, (RT).

Mimosa strigillosa J. Torrey & A. Gray. Pink sensitivebrier, (DS).

Parkinsonia aculeata C. Linnaeus. Retama, (BG, RT, CM, DS).

Prosopis glandulosa J. Torrey. Mesquite, (BG, CM, RT, DS).

Prosopis reptans G. Bentham var. *cinerascens* (A. Gray) A. Burkhart. Creeping mesquite, tornillo, (RT, SF, CM, DS).

Sesbania drummondii (P. Rydberg) V. Cory. Drummond's rattlebush, poison bean, (RT).

Sesbania herbacea (P. Miller) R. McVaugh. Large-fruited rattlebush, (RT).

GENTIANACEAE

Eustoma exaltatum (C. Linnaeus) A. Salisbury *ex* G. Don. Tall prairie gentian, bluebell gentian, (RT, DS).

HYDROPHYLLACEAE

Nama hispidum A. Gray. Rough nama, (DS).

Nama jamaicense C. Linnaeus. Jamaican nama, (DS).

LAMIACEAE

Micromeria brownei (O. Swartz) G. Bentham var. *pilosiuscula* A. Gray. Browne's savory, (RT).

Salvia coccinea P. Buc'hoz *ex* A. Etlinger. Scarlet sage, (BG, RT).

Teucrium cubense N. von Jacquin. Germander, (BG, DS).

LYTHRACEAE

Lythrum alatum F. Pursh var. *lanceolatum* (S. Elliott) J. Torrey & A.

Gray *ex* J. Rothrock. Lance-leaf loosestrife, (RT, DS).

Lythrum californicum J. Torrey & A. Gray. California loosestrife, (RT, DS).

MALVACEAE

Abutilon trisulcatum (N. von Jacquin) I. Urban. Anglestem abutilon, (BG, DS).

Anoda pentaschista A. Gray. Field anoda, (DS).

Bastardia viscosa (C. Linnaeus) K. Kunth. Viscid bastardia, (BG).

Billieturnera helleri (J. Rose *ex* A. A. Heller) P. Fryxell. Coppery false fanpetals, (DS).

Malvastrum americanum (C. Linnaeus) J. Torrey. Rio Grande falsemallow, malva loca, (DS, RT).

Malvastrum coromandelianum (C. Linnaeus) C. Garcke. Three-lobe false-mallow, (DS, RT).

Rhynchosida physocalyx (A. Gray) P. Fryxell. Spear-leaf beaked fanpetals, (DS).

Sida abutifolia P. Miller. Spreading fanpetals, (DS).

Sida spinosa C. Linnaeus. Prickly fanpetals, (DS).

NYCTAGINACEAE

Acleisanthes obtusa (J. Choisy) P. Standley. Berlandier's trumpets, vine four o'clock, (BG).

NYMPHAEACEAE

Nymphaea elegans W. J. Hooker. Blue waterlily, (RT).

OLEACEAE

Forestiera angustifolia J. Torrey. Narrow-leaf elbowbush, desert olive, panalero, (BG).

ONAGRACEAE

Oenothera speciosa T. Nuttall. Showy evening-primrose, amapola del campo, (DS).

OXALIDACEAE

Oxalis dichondrifolia A. Gray. Ponyfoot-leaf woodsorrel, (TB, DS).

Oxalis stricta C. Linnaeus. Common yellow woodsorrel, (DS).

PASSIFLORACEAE

Passiflora foetida C. Linnaeus var. *gossypifolia* (N. Desvaux *ex* W.

Hamilton) M.T. Masters. Cotton-leaf passionflower vine, corona de cristo, (DS).

PHYTOLACCACEAE

Rivina humilis C. Linnaeus. Rouge-plant, pigeonberry, (BG).

PLANTAGINACEAE

Plantago rhodosperma J. Decaisne. Redseed plantain, (DS).

PLUMBAGINACEAE

Limonium carolinianum (T. Walter) N. Britton. Sea-lavender, marsh-rosemary, (SF, CM).

POLYGONACEAE

Rumex chrysocarpus G. Moris. Amnastla dock, (RT).

PORTULACACEAE

Portulaca oleracea C. Linnaeus. Purslane, (DS).
Portulaca pilosa C. Linnaeus. Chisme, (DS).
Portulaca umbraticola K. Kunth. Crowned wingpod purslane, (DS).
Talinum aurantiacum G. Engelmann. Orange flameflower, (BG).

PRIMULACEAE

Anagallis arvensis C. Linnaeus. Scarlet pimpernel, (DS, I).
Samolus ebracteatus K. Kunth subsp. *cuneatus* (J.K. Small) R. Kunth. Wedge-leaf brookweed, (RT).

RANUNCULACEAE

Clematis drummondii J. Torrey & A. Gray. Barbas de chivato, old man's-beard, (DS).

RHAMNACEAE

Condalia hookeri M. C. Johnston. Brasil, (BG).
Karwinskia humboldtiana (J. A. Schultes) J. Zuccarini. Coyotillo, (BG).
Ziziphus obtusifolia (W. J. Hooker *ex* J. Torrey & A. Gray) A. Gray. Lotebush, (BG).

RUBIACEAE

Spermacoce glabra A. Michaux. Smooth false buttonweed, (RT).

RUTACEAE

Zanthoxylum fagara (C. Linnaeus) C. Sargent. Colima, lime pricklyash, (BG).

SALICACEAE

Salix nigra H. Marshall. Black willow, (RT).

SAPOTACEAE

Sideroxylon celastrinum (K. Kunth) T. Pennington. La coma, (BG).

SCROPHULARIACEAE

Bacopa monnieri (C. Linnaeus) F. Pennell. Coastal water-hyssop, (RT).

Leucophyllum frutescens (J. Berlandier) I. M. Johnston. Cenizo, (BG).

Mecardonia procumbens (P. Miller) J. K. Small. Yellow-flowered mecardonia, (RT).

Veronica peregrina C. Linnaeus subsp. *xalapensis* (K. Kunth) F. Pennell. Purslane speedwell, (RT).

SIMAROUBACEAE

Castela erecta P. Turpin subsp. *texana* (J. Torrey & A. Gray) J. Rose. All-thorn goatbush, amargosa, (BG).

SOLANACEAE

Calibrachoa parviflora (A. L. de Jussieu) W. D'Arcy. Wild petunia, (DS, I).

Capsicum annuum C. Linnaeus var. *aviculare* (J. Dierbach) W. D'Arcy & W. Eshbaugh. Chilipiquín, (BG).

Chamaesaracha coronopus (M. Dunal) A. Gray. False nightshade, (DS)..

Lycium berlandieri M. Dunal. Berlandier's wolfberry, (BG).

Lycium carolinianum T. Walter var. *quadrifidum* (M. Dunal) C. Hitchcock. Coastal wolfberry, (RT, SF, CM).

Margaranthus solanaceus D. von Schlechtendal. Netted globeberry, (DS).

Physalis cinerascens (M. Dunal) A. Hitchcock var. *cinerascens* Ground cherry, (DS).

Physalis pubescens C. Linnaeus. Downy groundcherry, (DS).

Solanum americanum P. Miller. American black nightshade, (RT, DS).

Solanum campechiense C. Linnaeus. Red-berry nightshade, (RT).

Solanum elaeagnifolium A. Cavanilles. Silver-leaf nightshade, trompillo, (DS).

Solanum triquetrum A. Cavanilles. Texas nightshade, (DS).

STERCULIACEAE

Melochia pyramidata C. Linnaeus. Angle-pod broomweed, (BG, RT).

TAMARICACEAE

Tamarix aphylla (C. Linnaeus) G. Karsten. Athel tamarisk, (DS, I).

ULMACEAE

Celtis pallida J. Torrey. Spiny hackberry, granjeno, (BG).

URTICACEAE

Parietaria pensylvanica G. H. Muhlenberg *ex* C. von Willdenow. Pellitory, (DS).

Urtica chamaedryoides F. Pursh. Heart-leaf stinging nettle, (RT, DS).

VERBENACEAE

Aloysia gratissima (J. Gillies & W.J. Hooker) N. Troncoso. White brush, (BG).

Glandularia bipinnatifida (T. Nuttall) T. Nuttall. Dakota mock vervain, (DS).

Glandularia quadrangulata (A.A. Heller) R. Umber. Gulf coast mock vervain, (DS).

Lantana achyranthifolia R. Desfontaines. Desert lantana, (BG).

Lantana urticoides A. von Hayek. Texas lantana, (BG, DS).

Phyla nodiflora (C. Linnaeus) E. Greene. Texas frog-fruit, (RT, DS).

Verbena brasiliensis J. Velloso de Miranda. Brazilian vervain, (DS, I).

Verbena canescens K. Kunth. Gray vervain, (DS).

Verbena halei J.K. Small. Texas vervain, (DS).

Verbena runyonii H. Moldenke. Runyon's vervain, (DS).

VISCACEAE

Phoradendron tomentosum (A.P. de Candolle) G. Engelmann *ex* A. Gray. Mistletoe, (BG).

VITACEAE

Cissus incisa C. Des Moulins. Possumgrape, (DS).

LILIOPSIDA (MONOCOTS)

AGAVACEAE

Agave americana C. Linnaeus. Century plant, (DS).

Yucca treculeana E. Carrière. Spanish dagger, palma pita, (BG).

ALISMATACEAE

Echinodorus beteroi (K. Sprengel) N. Fasset. Beaked burhead, (RT).

Sagittaria longiloba G. Engelmann *ex* J. Torrey. Long-lobe arrowhead, (RT).

ALLIACEAE

Nothoscordum bivalve (C. Linnaeus) N. Britton. Crow-poison, (BG, DS).

AMARYLLIDACEAE

Cooperia sp. Rainlily, (BG, DS).

BROMELIACEAE

Tillandsia baileyi J. Rose *ex* J.K. Small. Bailey's ball moss, (BG, TOES V. Watch list).

Tillandsia recurvata (C. Linnaeus) C. Linnaeus. Ball moss, (BG).

COMMELINACEAE

Callisia micrantha (J. Torrey) D. Hunt. Small-flowered roseling, (BG).

Commelina erecta C. Linnaeus var. *angustifolia* (A. Michaux) M. Fernald. Widow's tears, (DS).

CYPERACEAE

Bolboschoenus maritimus (C. Linnaeus) E. Palla subsp. *paludosus* (A. Nelson) T. Koyama. Prairie bulrush, (RT).

Cyperus articulatus C. Linnaeus. Jointed flat-sedge, (RT).

Cyperus esculentus C. Linnaeus. Yellow nutgrass, (RT).

Cyperus retroflexus S. Buckley. Backward-flexed flat-sedge, (DS).

Cyperus sp. Flat-sedge, (DS).

Eleocharis acicularis (C. Linnaeus) J.J. Röemer & J.A. Schultes.

Needle spikerush, (RT).

Eleocharis austrotexana M.C. Johnston. South Texas spikerush, (RT).

LEMNACEAE

Lemna minuta K. Kunth. Least duckweed, (RT).

POACEAE (Gramineae)

Aristida purpurea T. Nuttall var. *longiseta* (E. von Steudel) G. Vasey. Red threeawn, (DS).

Bothriochloa laguroides (A.P. de Candolle) W. Herter subsp. *torreyana* (E. von Steudel) K. Allred & F. Gould. Torrey's silver beard-grass, (BG).

Bouteloua trifida G. Thurber. Red grama, (BG).

Buchloë dactyloides (T. Nuttall) G. Engelmann. Buffalo-grass, (BG).

Chloris barbata O. Swartz. Bearded windmill-grass, (DS).

Chloris ciliata O. Swartz. Fringed windmill-grass, (DS).

Chloris x *subdolichostachya* J.K.A. Müller. Nash's windmill-grass, (BG, DS).

Cynodon dactylon (C. Linnaeus) C. Persoon. Bermuda-grass, (DS, I).

Dichanthium annulatum (P. Forsskål) O. Stapf. Kleberg's bluestem, (DS, I).

Dichanthium aristatum (J. Poiret) C. Hubbard. Angleton bluestem, (DS, I).

Dichanthium sericeum (R. Brown) A. Camus. Silky bluestem, (DS, I).

Digitaria californica (G. Bentham) J. Henrard. California cottontop, (BG).

Digitaria pubiflora (G. Vasey) J. Wipff. Carolina crab-grass, (BG).

Enteropogon chlorideus (J. Presl) W. Clayton. Bury-seed umbrella-grass, (BG).

Eragrostis reptans (A. Michaux) C. Nees von Esenbeck. Creeping love-grass, (RT).

Eriochloa pseudoacrotricha (O. Stapf *ex* Thellung) C. Hubbard *ex* S.T. Blake. Mock hairy-end cupgrass, (RT, DS, I).

Eriochloa punctata (C. Linnaeus) N. Desvaux *ex* W. Hamilton. Spotted cup-grass, (RT).

Leptochloa dubia (K. Kunth) C. Nees von Esenbeck. Green sprangletop, (BG).

Leptochloa fusca (C. Linnaeus) K. Kunth subsp. *uninervia* (J. Presl) N. Snow. Mexican sprangletop, (RT).

Leptochloa nealleyi G. Vasey. Neally's sprangletop, (RT).

Leptochloa panicea (A. Retzius) J. Ohwi subsp. *brachiata* (E. von Steudel) N. Snow. Sprangletop, (DS).

Monanthochloë littoralis G. Englemann. Shore-grass, (SF, CM).

Panicum hallii G. Vasey var. *filipes* (L. Lamson-Scribner) F. Waller. Filly panicum, (BG).

Pappophorum vaginatum S. Buckley. Whip-lash pappus-grass, (BG).

Paspalidium geminatum (P. Forsskål) O. Stapf. Egyptian paspalidium, (RT).

Paspalum denticulatum K. von Trinius. Long-tom, (RT).

Paspalum pubiflorum F. Ruprecht *ex* E. Fournier. Hairyseed paspalum, (DS).

Pennisetum ciliare (C. Linnaeus) J. Link. Buffel-grass, (DS, I).

Setaria leucopila (F. Lamson-Scribner & E. Merrill) K. Schumann. Plains bristle-grass, (BG).

Spartina spartinae (K. von Trinius) E. Merrill *ex* A. S. Hitchcock. Gulf cord-grass, (CM).

Sporobolus pyramidatus (J. de Lamarck) A.S. Hitchcock. Whorled drop-seed, (DS, SF).

Sporobolus virginicus (C. Linnaeus) K. Kunth. Sea-shore drop-seed, (SF, CM).

Trichloris pluriflora E. Fournier. Multi-flowered false Rhode's-grass, (BG).

Tridens albescens (G. Vasey) E. Wooton & P. Standley. White tridens, (BG).

Tridens eragrostoides (G. Vasey) & F. Lamson-Scribner) G. Nash. Love-grass tridens, (BG).

Tridens texanus (S. Watson) G. Nash. Texas tridens, (BG).

Urochloa fasciculata (O. Swartz) R.D. Webster. Brown-top liver-seed grass, (DS).

Urochloa maxima (N. von Jacquin) R.E. Webster. Guinea grass, (DS, I).

Urochloa panicoides A. Palisot de Beauvois. Panic liver-seed grass, (A federally listed noxious weed, DS, I).

Urochloa texana (S. Buckley) R. D. Webster. Texas millet, (DS).

PONTEDERIACEAE

Heteranthera dubia (N. von Jacquin) C. MacMillan. Water stargrass, (RT).

TYPHACEAE

Typha domingensis C. Persoon. Narrow-leaf cat-tail, (RT).

The flora of PANBHS represents about one-fourth (24.2%) of the total flora (1,004 species) of the Rio Grande Delta and the lower Rio Grande Valley. Seven hundred thirty-two species of dicots representing 410 genera and 92 families were catalogued by Richardson (1995) in the Rio Grande Delta. The Asteraceae (115 species), Fabaceae (74 species), and Euphorbiaceae (47 species) are the most common families, and they represent almost one-third (32.2%) of the species richness. Richardson (1995) and Lonard (1993) listed 17 families, 99 genera and 269 species of monocots. The Poaceae (188 species) and Cyperaceae (41 species) account for 85.1% of the species richness of monocots in the area.

No rare, threatened, or endangered species were catalogued. However, *Tillandsia baileyi*, epiphytic on *Chloroleucon ebano* in an upland brush thicket, is listed as a category V "watch list" plant by the Texas Organization for Endangered Species. Britton & Morton (1989) listed *Lycium carolinianum* var. *quadrifidum* only along bayshores in Texas. However, it was common in resaca basins and salt flats.

Several introduced potentially invasive grasses including *Dichanthium annulatum, Dichanthium aristatum, Pennisetum ciliare, Urochloa maxima* and *Urochloa panicoides*, occur in the core battlefield site and in disturbed sites along roads and trails. *Urochloa panicoides* is a federally listed noxious weed. No plans have been formulated to eliminate these species. *Kalanchoë delagoënsis* is confined to a small area near a parking lot and could be removed by hand.

Historical accounts indicate that *S. spartinae* was the most important species in the core battlefield in 1846 (Sanchez 1985). Optimal development of a Gulf Cordgrass community occurs in saline, hydric soils where water levels range from 30 cm below the soil surface to 4 cm above ground level (Oefinger & Scifres 1977; Scifres et al. 1980). Periodic flooding of the Rio Grande has been eliminated by dams and drainage projects. Only occasional flooding occurs at PANBHS as a result of rainfall rather than flooding from the river. Implementation of a plan to restore *S. spartinae* at the battlefield site will require removal of excess sediment from resaca channels, and cyclic flooding will be a prerequisite to restore hydrologic processes. Therefore, it is doubtful that the core battlefield can be restored to a landscape similar to conditions that prevailed in 1846.

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SPATIAL AND TEMPORAL ABIOTIC CHANGES ALONG A CANOPY TO INTERCANOPY GRADIENT IN CENTRAL TEXAS *JUNIPERUS ASHEI* WOODLANDS

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Abstract.-*Juniperus ashei* (ashe juniper), in the southern Edwards Plateau region of central Texas, exhibits both spatial and temporal trends in seedling demography, emergence, growth and physiology which vary in relation to patterns of woodland overstory: the canopy patches of woody plants vs. the intercanopy patches of grasses and herbs between them. This study reports gradients of abiotic factors found from below *J. ashei* canopy trees into associated intercanopy patches. There were significant differences in soil organic content, soil field capacity, soil temperature, soil water content and surface light levels along this gradient from April through December 1997, but not soil depth. Mean soil organic content was highest under the canopy (32.0 ± 6.9%) and lowest in the intercanopy patch (12.5 ± 0.8%) as was the field capacity (108.5 ± 2.8% and 82.9 ± 1.6% respectively). Mean midday light levels were highest in the intercanopy (1183 ± 149 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and were lowest below the canopy (346 ± 99 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and 219 ± 77 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, canopy and mid-canopy respectively). Mean midday soil temperature varied seasonally, but was highest in the intercanopy (32.6 ± 2.1°C) and lowest at the canopy edge (27.6 ± 1.4°C). Mean soil water content also varied seasonally (with rainfall), and was highest under the canopy (43.4 ± 3.0%) and lowest in the intercanopy (30.3 ± 2.1%). Reduced light levels under the canopy, coupled with high soil organic content may ameliorate high soil temperatures and promote higher soil water content, possibly resulting in reduced water stress and increased *J. ashei* seedling survival. However, increased growth at the canopy edge may be attributed to increased surface light levels at this location. Low seedling emergence and survival in the intercanopy patch may be due to a combination of factors, in particular seasonal high soil surface temperatures and low soil water content.

The Edwards Plateau of central Texas comprises approximately 10 million hectares (Gould 1975; Diamond et al. 1995). It is bordered on the north by the High Plains and Rolling Plains, on the west by the Trans-Pecos Region, and on the southern and eastern boundaries by the Balconies Escarpment. In many parts of the Edwards Plateau, especially in the southern portion, *Juniperus ashei* is a dominant woodland species (Van Auken et al. 1981; Van Auken 1988). *Juniperus ashei* co-occurs with *Quercus fusiformis* (= *Q. virginiana*, Hatch et al. 1990), *Q. texana* and *Diospyros texana* in these woodlands (Van Auken et al. 1981).

Juniperus ashei is an evergreen aromatic shrub or small tree (< 9 m) with one or several trunks (Correll & Johnson 1979); it is fire sensitive (Foster 1917; Johnson & Alexander 1974; Fuhlendorf et al. 1996) and likely drought tolerant (Fonteyn et al. 1985; Wayne & Van Auken

2002). Densities of *J. ashei* in these woodlands in the southern part of the Edwards Plateau are ≈ 1500 trees/ha (Van Auken et al. 1981; Van Auken 1988) with an estimated canopy cover of 40 to 90% (Van Auken et al. 1981; Smeins & Merrill 1988). *Carex planostachys* (cedar sedge) occurs under the *Juniperus* canopy and is an herbaceous species with high cover and wide distribution in these woodlands (Wayne 2000).

These central Texas *Juniperus* woodlands are fairly open in some places and are associated with glades or small grasslands (Quarterman 1950; Baskin & Baskin 1978, 2000; Quarterman et al. 1993; Terletzky & Van Auken 1996). These open areas are more correctly referred to as intercanopy patches (Breshears et al. 1997a; 1997b; Martens et al. 1997; Reid et al. 1999; Van Auken 2000a; Ware 2002). Additionally, these intercanopy patches may have a high or low cover of herbaceous plants which appears to be related to soil depth (Terletzky & Van Auken 1996; Van Auken 2000a).

Juniperus ashei was present historically in the southern Edwards Plateau region (Foster 1917; Diamond et al. 1995), in areas that offered protection from grassland fires such as steep rocky slopes or outcrops. However, *J. ashei*, like many other woody species, has increased its density in grasslands over the past 100 to 150 years (Bray 1904; Foster 1917; Diamond 1997; Scholes & Archer 1997; Brown & Archer 1999). Causes of this encroachment are likely due to continuous, heavy grazing by domestic herbivores leading to reduced light fluffy fuel and decreased fire frequency (McPherson et al. 1988; Riskind & Diamond 1988; Diamond et al. 1995; Fuhlendorf et al. 1996; Van Auken 2000b). Anthropogenic factors such as elevated levels of CO_2 and climatic change are often cited (see Polley et al. 1996) as possible causes of woody plant encroachment, but are not necessary to explain these community changes (Archer et al. 1995; Van Auken 2000b). It is unknown if *J. ashei* is continuing to encroach into the remaining intercanopy patches, but predictive models indicate that grasslands are maintained with frequent fires (Fuhlendorf et al. 1996).

The physiology and demography of *J. ashei* in central Texas woodlands and intercanopy patches is poorly understood. Mature *J. ashei* trees exhibit low stomatal conductance and carbon assimilation during summer drought (Owens & Schreiber 1992; Owens 1996) and high water stress (Fonteyn et al. 1985; Wayne & Van Auken 2002). These trends are reversed in the fall through spring when temperatures are lower and the soil water content is higher. Density of *J. ashei* seedlings in these woodlands appear to be influenced by spatial and temporal gradients of abiotic factors (Wayne & Van Auken 2002).

In addition, seedling emergence is highest in early winter through early spring; with most emergences occurring beneath the woodland canopy (Jackson & Van Auken 1997), a smaller number of seedling emergences occur at the canopy edge and few in the intercanopy patch. Most *J. ashei* seedling mortality coincides with summer drought, with the highest mortality in the intercanopy patch, followed by the canopy edge and lowest mortality below the canopy (Jackson & Van Auken 1997; Van Auken et al. 2004). Seedling growth rates on the other hand are highest at the canopy edge and reduced under the canopy. *Juniperus ashei* seedling water stress is highest during summer drought (< -7.0 MPa), but recovers quickly with small rainfall events (Wayne & Van Auken 2002). *Juniperus ashei* seedlings at the canopy edge exhibit greater water stress than canopy seedlings during summer drought, but no data is available for seedlings in the intercanopy patches. *Carex planostachys*, a co-occurring sub-canopy herbaceous species appears to have a water stress response similar to that of *J. ashei* seedlings (Wayne 2000).

Although several studies have described plant communities in various parts of the Edwards Plateau Region (Van Auken et al. 1981; Van Auken 1988; Terletzky & Van Auken 1996; Van Auken 2000a) none have reported the cause of differences in *J. ashei* seedling survival or growth, but have suggested various abiotic factors. Van Auken (2000a) reported the presence of a soil depth gradient. Wayne & Van Auken (2002) indicated a xylem water potential gradient in *J. ashei* woodlands. It is hypothesized that gradients of other abiotic factors occur. These gradients may be responsible for the variation in species density and cover in these *Juniperus* woodlands. The purpose of this study is to quantify the magnitude and direction of the abiotic gradients from beneath the *J. ashei* canopy into the intercanopy.

MATERIALS AND METHODS

This study was conducted April through December 1997 on a 1760 m^2 site in Eisenhower Park, a San Antonio, Texas city park, in northern Bexar County (98°34'26" W and 29°37'19" N), located on the southern Edwards Plateau. The park is 128 ha and maintained as a natural area without domestic grazing (> 50 yrs, Eric Lautzenheiser pers. comm.). The site is near the Balconies fault zone and approximately 5 km east of the University of Texas at San Antonio campus. A site was selected representative of a *J. ashei* woodland with an associated intercanopy patch that appeared to be infrequently accessed by humans. Soil is a clayey-skeletal, smectitic, thermic lithic calciustoll (United States Department of Agriculture 2000) in the Tarrant association - rolling - with a slope of 4.5° to 13.5°. Three horizons occur that consist of shallow, clayey, weakly calcareous soil, developed over hard limestone with scattered stones and gravel. The surface horizon ranges from 0 cm to 25 cm in thickness. The subsurface is approximately 20 cm thick, heavily fractured limestone over limestone bedrock (Taylor et al. 1962). Regional climate is classified as subtropical - subhumid with a mean annual temperature of 20°C (Arbingast et al. 1976). Monthly mean temperature ranges from 9.6°C in January to 29.4°C in July (National Oceanic and Atmospheric Administration 1999). Annual precipitation in the study area is 78.7 cm, with two peaks occurring in May and September with monthly means of 10.7 cm and 8.7 cm, respectively. During the study, precipitation was above normal for 1997 at 85.6 cm (National Oceanic and Atmospheric Administration 1999), with a low of 0.0 cm in July, negligible in August, and a high of 18.5 cm in June.

The area vegetation is juniper/oak woodland representative of similar woodlands found throughout this region (Van Auken et al. 1981). The predominant woody vegetation is *J. ashei* and *Quercus virginiana* (live oak). Other woody species reported from the area are *Q. texana* (Spanish oak), *Celtis laevagata* (hackberry), *Diospyros texana* (Texas persimmon), *Berberis trifoliata* (agarita) and *Rhus virens* (evergreen sumac) (Van Auken et al. 1980; 1981; Terletzky & Van Auken 1996). *Carex planostachys* (Correll & Johnston 1979) was the dominant herbaceous species below the woodland canopy. The major herbaceous species in the intercanopy patches were *Aristida longiseta* (red three-awn), *Bouteloua curtipendula* (side-oats gramma), other C_3 and C_4 grasses and a variety of herbaceous annuals (Fowler & Dunlap 1986; Van Auken 2000a).

Measurements of surface and subsurface soil moisture, soil temperature, soil organic content and field capacity were made at each of five positions along six parallel northeasterly transects (41° azimuth). Frequency and time of measurements are indicated for each factor. The surface horizon of the soil was the upper 2 cm of soil and the subsurface horizon was the lowest 2 cm of soil adjacent to the bedrock. Each transect was 15 m in length and at least 3 m from an adjacent transect. A plumb line dropped from the outermost branch of mature *J. ashei* trees (2 m above the ground, located directly above each transect) was used to locate the canopy edge (drip line). Surveyor tapes were used to establish the following sampling positions: 10 m inside the canopy

(canopy), 5 m inside the canopy (mid-canopy), 0 m inside the canopy (canopy edge), 2.5 m outside the canopy (mid-intercanopy) and 5 m outside the canopy (intercanopy). There were 6 transects by 5 sampling positions for the surface horizon and for the subsurface horizon. Significant differences in soil moisture and soil temperature were detected between the surface and subsurface horizons (*ANOVA*, SAS Institute 1989). Because the overall mean values between the surface and subsurface were small (< 2°C for soil temperature and < 5% for soil moisture) surface measurements will be the main focus of this paper.

Soil moisture was determined using the gravimetric procedure and reported as the percent water in the sample on a dry-mass basis (Pearcy 1989; United States Department of Agriculture 1996; Jackson et al. 2000). Soil samples were collected along each transect ($n = 6$), at each position ($n = 5$) for the surface and bedrock horizons ($n = 2$) in April, May, July, August, September, October, and twice in December ($n = 8$ for a total of 480 samples). Stones and organic litter were removed from the soil surface; soil samples were collected and sealed in plastic bags for transport to the lab. Approximately 40 g of soil was placed in a pre-weighed aluminum planchet, weighed and oven dried at 100°C to a constant mass.

Soil temperature was measured within two hours after solar noon on the same dates as soil moisture (with the exception of May and the latter December measurement ($n = 6$ months for a total of 360 samples) using 15 cm long, probe type, analog soil thermometers (Broadbent 1965; Larcher 1995). Surface temperature was measured by inserting the probe 1 to 2 cm into the soil and recording the temperature after five minutes of equilibration. Subsurface temperature was measured by excavating soil to the bedrock and inserting the probe into the lowest 2 cm of exposed soil.

Surface light levels (photosynthetically active photon flux density, $\lambda = 400$ to 700 nm,) were measured at solar noon on cloudless days in July, August, October and December ($n = 4$ months for a total of 120 samples) with a LI-COR® (LI-COR Inc., Lincoln, Nebraska) LI-190 SA integrating quantum sensor. Light levels were recorded with a LI-COR® LI-1000 data logger in instantaneous mode with 60 s averaging at 5 s intervals. No measurements were made April through June 1997 because of overcast conditions. The quantum sensor was placed level on bare ground at each position and no attempt was made to move or disrupt any woody or herbaceous vegetation over the sensor.

The soil depth profile was measured at the conclusion of this study to minimize potential disturbances to the plants and soil of the study area (Broadbent 1965). Surface litter was removed and measurements were made along each transect at 0.5 m intervals (*n* = 186) using a 60 by 1 cm rebar driven vertically into the ground until it would not penetrate any deeper. The distance from the top of the rod to the ground was measured and subtracted from 60 cm to obtain the soil depth. Periodically, the rebar was re-measured to ensure the length did not change.

Percent soil organic content was determined for the surface and bedrock horizons (*n* = 2 for a total of 60 samples) using the loss-on-ignition procedure (Broadbent 1965; United States Department of Agriculture 1996). Excess soil collected from the December 1997 soil moisture sampling was used for the determination of the soil organic content. The soil was air-dried and sieved (#10 mesh), tested for the presence of carbonates (United States Department of Agriculture 1996), oven dried at 90°C and incinerated in a Fischer Muffle Furnace (Model 58) at 600°C for 3 hours. The test for presence of carbonates was negative.

Determination of percent field capacity (Broadbent 1965) for the surface and bedrock horizon was made using sieved (#10 mesh), air-dried soil, however only four transects were utilized (*n* = 2 for a total of 40 samples). The soil was placed level into a perforated aluminum planchet lined with # 1 filter paper, thoroughly wetted for 12 h and drained for 20 minutes. The soil was then oven dried to a constant mass at 100°C.

The experimental design was factorial for surface light, soil water and soil temperature (position by date). Data were transformed as needed prior to statistical analysis and analyzed with *ANOVA* (SAS Institute 1989). When significant main effects were detected, data were subset to examine temporal and spatial differences using *ANOVA* and the Scheffé multiple comparison test ($\alpha = 0.05$, SAS Institute 1989). Mean surface values were pooled temporal data (all dates) for each transect position to show the overall spatial differences in surface values. Although *ANOVA* may indicate that a significant difference occurred the Scheffé multiple comparison test may indicate otherwise because of its conservative nature in computing the minimum significant difference (three examples occurred, SAS Institute 1989; Sokal & Rohlf 1995).

RESULTS

Soil depth was erratic and did not vary significantly from the canopy to the intercanopy patch ($F = 0.69$, $P = 0.8858$, Fig. 1). Mean soil depth (± *SE*) ranged from 9.9 ± 2.3 cm under the full canopy to 7.1

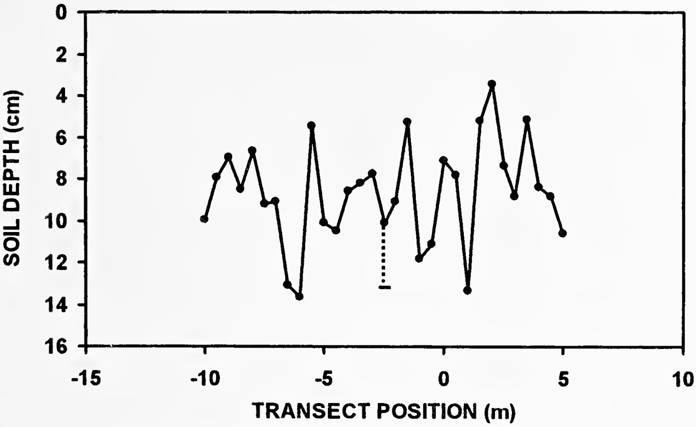

Figure 1. Mean soil depth profile (surface to bedrock, cm) measured at 0.5 m intervals along the canopy to intercanopy gradient (n = 6 transects) in the *Juniperus ashei* woodland. Lower bar with dotted line is an example standard error bar. Transect position (x-axis) is in meters from the canopy edge: canopy (-10), mid-canopy (-5), canopy edge (0), mid-intercanopy (2.5) and intercanopy (5). P-value for the *ANOVA* indicated no significant difference in positions.

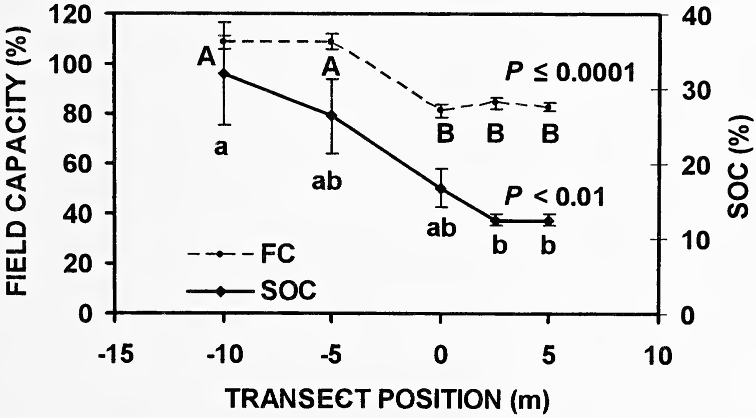

Figure 2. Spatial differences in mean (± *SE*) percent soil organic content and percent field capacity at the surface horizon. P-values indicated are for individual *ANOVA*'s. Transect position (x-axis) is in meters from the canopy edge: canopy (-10), mid-canopy (-5), canopy edge (0), mid-intercanopy (2.5) and intercanopy (5). Means within a measured parameter with different letters are significantly different (Scheffé multiple comparison test).

± 2.1 cm at the canopy edge and 10.6 ± 3.1 cm in the intercanopy patch. Soil depth ranged from zero to 40 cm and the overall mean depth was 9.2 ± 2.5 cm.

Overall mean soil organic content varied significantly by position (F = 8.59, P = 0.0001) and ranged from 32.0 ± 6.9% under the full canopy (Fig. 2) to 16.8 ± 2.6% at the canopy edge and 12.5 ± 0.8%

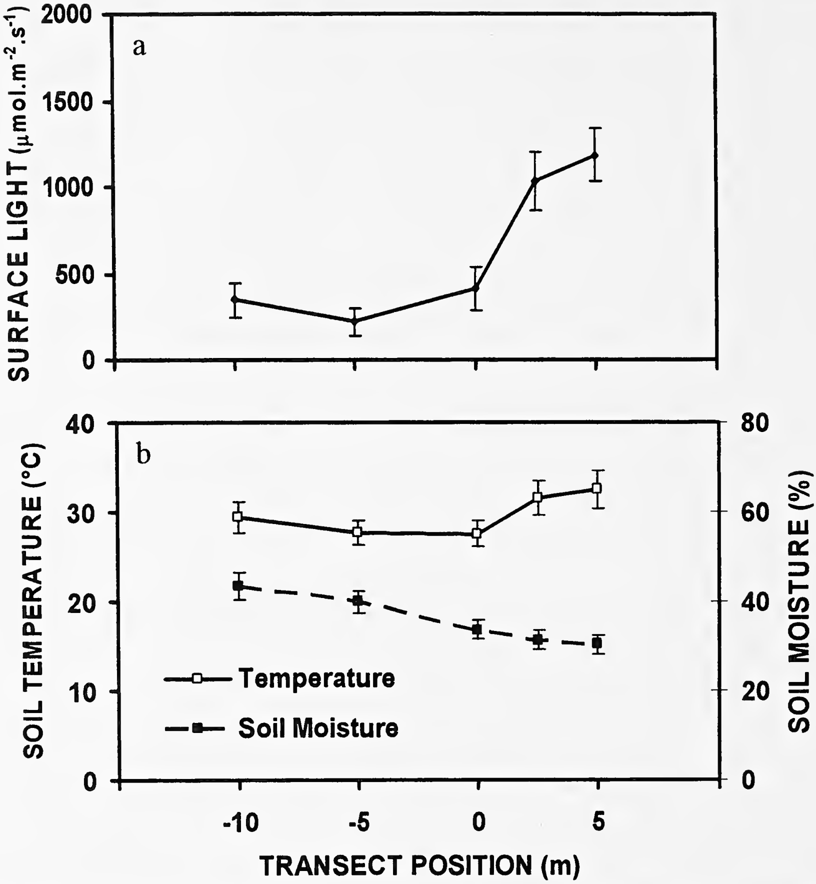

Figure 3. Yearly mean (± *SE*) surface gradient (n = 6 transects) from below the *Juniperus* canopy into the intercanopy (n = 5 positions) for (a) surface light levels (μmol • m^{-2} • s^{-1}) and (b) surface soil temperature (°C) and surface soil moisture (%). Light levels were measured at solar noon on cloudless days in July, August, October and December 1997 (n = 4). Soil temperature was measured within two hours after solar noon in April, July, August, September, October and December (n = 6). Soil moisture was measured in April, May, July, August, September, October and twice in December (n = 8). Transect position (x-axis) is in meters from the canopy edge: canopy (-10), mid-canopy (-5), canopy edge (0), mid-intercanopy (2.5) and intercanopy (5).

in the intercanopy patch. The Scheffé multiple comparison test indicated there was a significant difference in mean soil organic content between the canopy position and both patch positions, but no significant difference between the mid-canopy and the canopy edge positions.

Overall field capacity varied significantly by position (F = 31.90, P = 0.0001) and ranged from 108.5 ± 2.8% under the *Juniperus* woodland canopy (Fig. 2) to 81.3 ± 2.9% at the canopy edge and 82.9 ± 1.6% in the intercanopy. The Scheffé multiple comparison test indicated that there was not a significant difference between the canopy and mid-

Table 1. *F*-tables and significance levels from three separate analyses of variance, examining (a) light levels, (b) soil temperature and (c) % soil moisture. Variables examined include the overall model, date (D), transect position (P), soil horizon (H) and the various two and three-way interactions. Transect positions are canopy, mid-canopy, canopy edge, mid-intercanopy patch and intercanopy patch. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P \leq 0.0001$ and NS = not significantly different.

(a) Light levels.

Source	*df*	*F*
Model	19	6.67****
Date (D)	3	13.92****
Position (P)	4	16.37****
D*P	12	1.62NS

(b) Soil temperature.

Source	*df*	*F*
Model	59	36.90****
Date (D)	5	365.00****
Horizon (H)	1	78.55****
Position (P)	4	19.80****
D*H	5	2.69*
D*P	20	8.38****
H*P	4	0.88NS
H*D*P	20	0.49NS

(c) Soil moisture.

Source	*df*	*F*
Model	79	23.77****
Date (D)	7	218.81****
Horizon (H)	1	1.32NS
Position (P)	4	39.28****
D*H	7	9.99****
D*P	28	5.66***
H*P	4	2.86****
H*D*P	28	0.53NS

canopy positions but they differed from all other positions. There was no significant difference between means for the canopy edge and the intercanopy positions.

The overall trend in surface light levels, soil temperature and soil moisture are best observed by pooling all surface temporal data for each position (Fig. 3). Mean surface light levels varied significantly by date and position, but the interaction term was not significant (Table 1a). Spatially, surface light levels (Fig. 3a) were lowest below the canopy and mid-canopy positions, 346 ± 99 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 219 ± 77 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ respectively, were intermediate at the canopy edge and highest in the intercanopy (1183 ± 149 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Mean soil temperature varied significantly by date, horizon, and position, with two significant two-way interactions (Table 1b). The significant interactions were date by horizon and date by position, but the three-way interaction was not significant. Spatially, mean yearly surface temperatures (Fig. 3b) were lowest at the canopy edge (27.6 ± 1.4°C), intermediate below the canopy (29.5 ± 1.8°C) and highest in the intercanopy (32.6 ± 2.1°C). Mean soil moisture varied significantly by date and position, with 3 significant two-way interactions (Table 1c). The three-way interaction was not significant. The general spatial trend for surface soil moisture (Fig. 3b) was highest values below the canopy (43.4 ± 3.0%), intermediate values at the canopy edge (33.6 ± 2.2%) and lowest values in the intercanopy (30.3 ± 2.1%).

Surface light below the canopy did not vary significantly ($F = 1.98$,

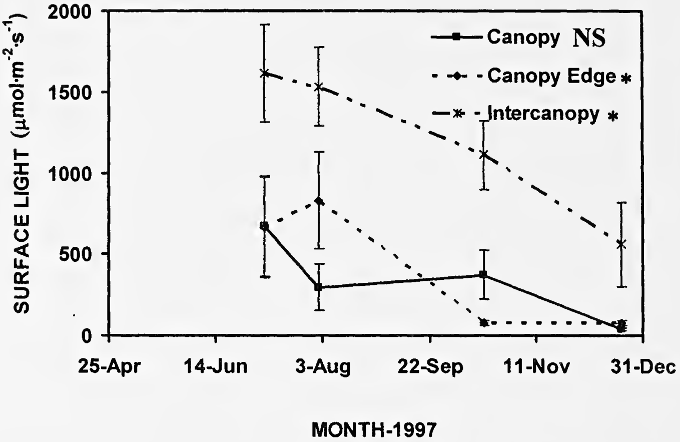

Figure 4. Temporal change in mean (± *SE*) surface light levels (µmol•m^{-2}•s^{-1}, $n = 6$ transects) below the canopy, at the canopy edge and in the intercanopy. Surface light was measured at solar noon on cloudless days in July, August, October and December 1997 ($n = 4$). Significance levels are indicated to the right of each position in the legend: NS is not significantly different, * is $P < 0.05$.

$P > 0.05$) and ranged from 675 ± 309 µmol·m^{-2}·s^{-1} in July (Fig. 4) to 39 ± 7 µmol·m^{-2}·s^{-1} in December. At the canopy edge, surface light varied significantly ($F = 3.37$, $P < 0.05$) and ranged from 666 ± 307 µmol·m^{-2}·s^{-1} in July to 78 ± 17 µmol·m^{-2}·s^{-1} in December; however, the Scheffé multiple comparison test did not detect any significant differences between dates. In the intercanopy, surface light varied significantly ($F = 6.88$, $P < 0.05$) ranging from 1614 ± 302 µmol·m^{-2}·s^{-1} in July to 479 ± 225 µmol·m^{-2}·s^{-1} in December. The August mean of 1531 ± 243 µmol·m^{-2}·s^{-1} was significantly different from the October and December means (Scheffé multiple comparison test), but not the July mean.

Temporal differences in mean surface temperature below the canopy varied significantly ($F = 41.37$, $P = 0.0001$) and ranged from 25.6 ± 1.9°C in May (Fig. 5a) to a high of 46.5 ± 3.3°C in August and a low of 16.0 ± 0.3°C in December. Mean surface temperature at the canopy edge varied significantly ($F = 53.83$, $P = 0.0001$) and ranged from 25.6 ± 0.7°C in May, increased to a high of 39.8 ± 2.2°C in July and a low of 16.3 ± 1.0°C in December. In the intercanopy, mean surface temperature varied significantly ($F = 32.66$, $P = 0.0001$) from 31.0 ± 0.7°C in May to a high of 48.8 ± 1.0°C in July and a low of 18.1 ± 0.8°C in December. Surface soil temperatures followed air temperatures (with a lag) and were high in July and August, and low in

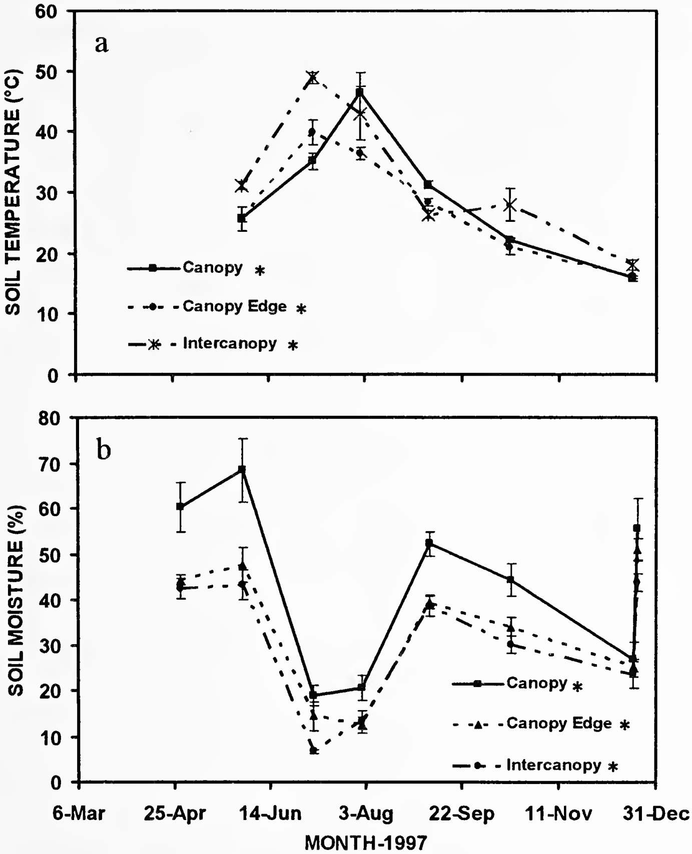

Figure 5. Temporal change in (a) mean (± *SE*) surface soil temperature (°C, $n = 6$ transects) and (b) mean (± *SE*) surface soil moisture (%, $n = 6$ transects) below the canopy, at the canopy edge and in the intercanopy. Temperature measurements were made within two hours after solar noon in April, July, August, September, October and December 1997 ($n = 6$). Soil moisture was measured in April, May, July, August, September, October and twice in December ($n = 8$). Significance levels are indicated to the right of each position in the legend: * is $P = 0.0001$.

December. The highest surface soil temperature was 48.8 ± 1.0°C in July in the intercanopy and the lowest was in December at 16.0 ± 0.3°C under the canopy. A significant decline from the high soil temperatures seen in July and August for all positions occurred in early September (≈ 12°C), coinciding with a 0.8 cm precipitation on the day preceding temperature measurements. After September soil temperature continued a significant decline to the low values observed in December for all positions except the intercanopy.

Temporal differences in mean surface soil moisture varied significantly below the canopy (F = 16.94, P = 0.0001) and ranged from 68.4 ± 7.0% in May (Fig. 5b) to a low of 18.9 ± 2.1% in July. Following the September precipitation, soil moisture increased to 52.2 ± 2.1%, followed by a second, but significant decline, and subsequent significant increase to 55.6 ± 6.8% after a late December precipitation event. The canopy edge and intercanopy locations also varied significantly (F = 42.5, P = 0.0001 and F = 84.2, P = 0.0001) and with the same significant decreases and increases seen below the canopy location. The canopy edge was at 47.7 ± 3.8% in May, decreased to a low of 12.5 ± 1.7% in August, increased to 39.5 ± 1.5% in September and was at 51.0 ± 2.4% in December. In the intercanopy, mean soil moisture was 43.2 ± 3.3% in May, declined to 6.8 ± 0.4% in July, increased to 38.6 ± 2.3% in September and was at 43.2 ± 2.0% in December. The overall temporal trend was high surface soil moisture in April-May and low surface soil moisture in June-August.

DISCUSSION

Soil depth in this study did not indicate a gradient from canopy to intercanopy locations. The very erratic soil depth observations from the *Juniperus* woodland canopy into the intercanopy patch were likely due to numerous surficial bedrock fractures (Davenport et al. 1996). At the northeastern extent of *J. ashei*'s range, calcareous derived soils are prevalent with rock outcrops common as well as fractures and pockets of deep soil (Quarterman et al. 1993; Ware 2002). These findings in *J. ashei* woodlands are not unlike those of *Pinus edulus*/*Juniperus monosperma* communities of New Mexico where soil depth fluctuated from 33 to 125 cm over distances of 10 m and without any significant differences between canopy and intercanopy locations (Davenport et al. 1996). Other *J. monosperma* communities such as those in Arizona (Johnsen 1962) and *J. pinchotii* in north Texas (McPherson et al. 1988) also occur over fractured bedrock. A similar trend of shallow soils over fractured bedrock has been reported for other locations in the Edwards Plateau (Foster 1917; Taylor et al. 1962; Owens & Schreiber 1992). However, gradients of soil depth have been reported in open patch communities in central Texas (Van Auken 2000a) and deeper soils have been confirmed in woodlands compared to intercanopy patches in this same area (Terletzky & Van Auken 1996; Ware 2002).

Specific spatial abiotic gradients were found during this study for soil organic content, field capacity, surface light levels, soil temperature and soil water content. The general trend was a decrease in soil organic content, field capacity, and soil water content from beneath the *Juniperus* canopy into the intercanopy patch. Surface light and soil temperature followed a reverse trend with high surface light levels and high soil temperatures in the intercanopy patch and lower values beneath the woodland canopy. Temporal differences in surface light, soil temperature and soil moisture were not presented for the mid-canopy and mid-intercanopy positions. However it was noted when examining individual dates the mid-canopy differed little from the canopy, and the mid-intercanopy differed little from the intercanopy (see Wayne 2000).

While surface litter, derived from the overstory, was not measured during this study it does have an influence on soil moisture content as it is incorporated into the soil (Knapp et al. 1993; Breshears et al. 1997b). It was noted that surface litter at the study site was ≈ 3 – 5 cm thick below the canopy, thin at the canopy edge, and absent in the intercanopy. In addition, the trend in soil organic content appears to coincide with areas of litter deposition and greater litter depth. High amounts of organic matter have a direct relationship with the soil water holding capacity and soil field capacity (Belsky & Canham 1994; Larcher 1995; Jackson et al. 2000). An additional characteristic of surface litter is that it insulates the soil from atmospheric temperature (Knapp et al. 1993; Breshears et al. 1998). It was demonstrated that soil organic content was low or absent in the intercanopy and increased from the canopy edge into the full canopy position. Similar trends in soil organic content and litter have been noted in African savannas with high levels found proximal to overstory trees (Belsky et al. 1989; 1993). In addition, the same has been found in *J. pinchotti* communities on the northern Edwards Plateau (Dye 1993; Dye et al. 1995) and west Texas (McPherson et al. 1991), piñon/juniper communities in New Mexico (Davenport et al. 1996) and other savanna communities (Belsky & Canham 1994).

Surface light levels were reduced beneath the *Juniperus* woodland likely due to light interception by the overstory canopy. This light reduction has been reported in other *J. ashei* communities on the Edwards Plateau (Yager & Smeins 1999), in oak savannas on the Edwards Plateau (Anderson et al. 2001), in *J. monosperma* communities in New Mexico (Breshears et al. 1997b; 1998; Martens et al. 2000) and in *J. virginiana* communities in the eastern North America (Joy & Young 2002). In piñon/juniper communities, differences in surface light levels are related mainly to canopy/intercanopy patch variation (i.e., overstory/no overstory) (Breshears et al. 1997b). Differences in light levels are not only spatial trends but temporal trends as well; and spatial effects are modified temporally. Light levels in piñon/juniper communities varied less temporally beneath the canopy than in the intercanopy patch, but the observed temporal differences were greatest during summer and least during winter. In *J. ashei* communities (this study), the spatial/temporal trends in light levels are similar to those reported in the *Juniperus* communities in New Mexico. Temporally light was highest during summer and reduced in winter. Light levels were higher in the intercanopy patch, intermediate at the canopy edge and lower in the canopy positions, which is consistent with piñon/juniper communities in western North America.

Soil temperatures from the canopy to the intercanopy patch followed a trend similar to the surface light gradient, lower soil temperatures below the canopy and highest temperatures in the intercanopy patch. This is consistent with *J. monosperma* communities in New Mexico (Breshears et al. 1997a) and *J. virginiaia* communities in eastern North America (Joy & Young 2002). Reduced canopy soil temperature is probably related to the interception of light by the canopy reducing heating of the soil by solar radiation (Helgerson 1990; Belsky et al. 1993; Breshears et al. 1997b). In addition, surface litter probably provides insulation of the soil from atmospheric temperature (Knapp et al. 1993; Breshears et al. 1998). Conversely, the higher soil temperatures in the intercanopy patch are influenced by the lack of overstory shading and absence of surface litter (Breshears et al. 1998). Soil moisture was also higher below the *Juniperus* canopy and may also play a role in the reduced canopy soil temperatures. High soil moisture also appears to ameliorate high soil temperatures across the entire gradient as noted following small precipitation events (Berndtsson et al. 1996; Wayne & Van Auken 2002).

A specific temporal trend of variable soil temperature was also detected. Peak soil temperatures across the study site were reached in late August; these high temperatures were subsequently modified, ≈ 20°C, by a small precipitation event (0.8 cm) in early September followed by a continued seasonal decline, ≈ 10°C, from fall through winter. In addition, during fall and winter there was little difference in mean soil temperature along the gradient (see Wayne 2000). Piñon/juniper woodlands in New Mexico followed a similar temporal trend where soil temperatures were elevated in the intercanopy patch (relative to the canopy) during the summer and decline fall through winter (Breshears et al. 1998). Differences were attributed to seasonal air temperatures and the changing angle of the sun.

Trends in soil moisture along the canopy to intercanopy patch gradient were reversed from that described for surface soil temperatures, soil moisture was highest below the canopy and reduced in the intercanopy patch. The exception to this trend was noted after precipitation events when differences between positions were not apparent. Possible causes for differences in soil moisture have been mentioned previously; including the canopy intercepting light resulting in reduced soil temperatures and also the high litter content below the canopy further ameliorating evaporative loss (Yager & Smeins 1999; Anderson et al. 2001; Joy & Young 2002).

Some piñon/juniper woodlands (Breshears et al. 1997a; 1997b; 1998) and oak savannas (Anderson et al. 2001) have lower soil moisture below the canopy and canopy edge then the adjacent patch, but it is unclear whether this was due to canopy interception of rainfall and/or evapotranspiration. With regard to piñon/juniper woodlands the soil moisture trend varies with time such that either patch type, canopy or intercanopy, can have increased soil moisture at some point during the year (Breshears et al. 1997b). Thus, these central Texas *Juniperus* woodlands were dissimilar from those in New Mexico that had mostly higher soil moisture in the intercanopy. High soil organic content and litter cover below the canopy may account for greater water storage capacity (measured as field capacity, Fig. 2). Runoff during rainfall from small intercanopy areas into canopy areas (Wilcox 1994; Ware 2002) may also increase soil moisture below the canopy and redistribute sediment (and litter) from the intercanopy into the canopy (Reid et al. 1999). Temporally, soil moisture was found to be decreased from spring into summer after cessation of rainfall (from ≈ 53% to 13% soil moisture), but recharge occurred rapidly (from ≈ 13% to 44% soil moisture) after small precipitation events (Wayne 2000; Wayne & Van Auken 2002).

Throughout most of the year abiotic conditions at the canopy edge are intermediate (see Wayne 2000; Wayne & Van Auken 2002) to the canopy and patch positions. Differences in aboveground canopy cover appear to explain a considerable amount of the heterogeneity detected in abiotic factors along the gradients in these *Juniperus* woodlands (Breshears et al. 1997b). Soil depth was not significantly different in this study and does not seem to play a role in the abiotic gradients. Higher *J. ashei* seedling emergence and survival (Jackson & Van Auken 1997; Van Auken et al. 2004), and high predawn xylem water potential below the canopy (Wayne & Van Auken 2002) seems related to the reduced stress attributable to slightly lower soil temperature and higher soil moisture. Thus, the canopy likely facilitates *J. ashei* in the early stages of its growth and development (Callaway et al. 1996; Joy & Young 2002). However, the canopy may also hinder *J. ashei* seedling growth due to light interception and reduced surface light levels (McKinley & Van Auken 2004), more so below the full canopy position then at the canopy edge.

Reduced availability of water and increased soil temperature appears to hinder seedling emergence and survival, while at the same time the increased light likely promotes seedling growth (Van Auken et al. 2004). This anomalous statement appears to explain differences in survival and growth of *J. ashei* seedlings in these different positions along the gradient. The intercanopy position exhibited the greatest soil temperature and lowest soil moisture, which seems to explain the low emergence and survival of *J. ashei* seedlings at this position along the gradient. Small precipitation events during late summer also appears to be important in reducing water stress of *J. ashei*, and other drought tolerant herbaceous species (see Wayne 2000) in these *Juniperus* communities (Fonteyn et al. 1985; Wayne & Van Auken 2002).

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TEXAS J. SCI. 56(1):55-62 FEBRUARY, 2004

REPRODUCTIVE CYCLE OF THE SIDEWINDER, *CROTALUS CERASTES* (SERPENTES: VIPERIDAE), FROM CALIFORNIA

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Abstract.—Reproductive tissue was examined from 159 museum specimens of *Crotalus cerastes* from California. Males follow a seasonal testicular cycle with sperm produced June-October; regressed testes were present March-June and October. Timing of this cycle is similar to that of other North American rattlesnakes. Sperm were present in the vasa deferentia March-October. Mean litter size for 26 *C. cerastes* was 7.96 ± 2.9 *SD*, range = 3-14. The number of females that were gravid (enlarged follicles > 8 mm or oviductal eggs) during the April to August period of female reproductive activity was 28/53 (53%). The presence of females with early yolk deposition in April and May when other females were gravid suggests more than one reproductive season is needed to complete yolk deposition.

The sidewinder, *Crotalus cerastes*, ranges from southern Nevada, southern California, south-central Arizona and extreme southwestern Utah, south to northeastern Baja California and northwestern Sonora; it occurs from below sea level to around 1830 m and is most common where there are sand hummocks topped with creosote bushes or mesquite (Stebbins 2003). Information on reproduction in *C. cerastes* is summarized in Ernst & Ernst (2003). Reiserer (2001) reported on reproduction in *C. cerastes* but did not perform gonadal histology. The purpose of this paper is to provide information on the reproductive cycle of *C. cerastes* from California from a histological examination of gonads from museum specimens.

MATERIAL AND METHODS

Sixty-two female (mean snout-vent length, SVL = 486 mm ± 53 *SD*, range = 375-592 mm) and 97 male (mean SVL = 446 mm ± 53 *SD*, range = 331-543 mm) *C. cerastes* were borrowed from the herpetology collections of the Natural History Museum of Los Angeles County, Los Angeles, California and the San Diego Society of Natural History, San Diego, California. Snakes were collected during 1935-1977. The left testis and part of the vas deferens were removed from males; the left ovary was removed from females for histological examination. Enlarged follicles (> 8 mm length) or oviductal eggs were counted; no histology was done on them. Tissues were embedded in paraffin and cut into sections at 5 μm. Slides were stained with Harris' hematoxylin, followed by eosin counterstain. Testes slides were examined to determine the stage of the spermatogenic cycle; vasa deferentia were examined for the presence of sperm. Ovary slides were examined for the presence of yolk deposition (= secondary vitellogenesis *sensu* Aldridge 1979a). Numbers of specimens examined by reproductive tissue were: testis = 97, vas deferens = 75, ovary = 34. The relationship between SVL and litter size was investigated by regression analysis. Unpaired *t*-tests were used to compare *C. cerastes* male and female mean body sizes (SVL), mean litter sizes with those from Klauber (1972), and mean litter sizes of northern versus southern populations from Klauber (1972).

Material examined.—Specimens of *Crotalus cerastes* from California (by county) examined from the herpetology collection of the Natural History Museum of Los Angeles County, Los Angeles (LACM) and the San Diego Society of Natural History (SDSNH). IMPERIAL: (LACM) 9202-9204, 52575, 52576, 64024, 104487, 104489, 104490. INYO: 52572, 104491, 116013, 116014; (SDSNH) 3219. KERN: (LACM) 52577, 52578, 63628, 63629, 63631, 63638, 63640-63642, 63644, 69905, 104493, 104495, 137690. LOS ANGELES: (LACM) 28006, 52579, 63447. RIVERSIDE: (LACM) 3025, 19936, 19938, 19942, 19944, 19945, 23235, 27996, 27998, 28000, 28001, 28783, 52582, 104499, 104500, 104507, 104508, 104511, 104512, 104519, 104523, 104542, 104547, 104549, 104552, 104555, 104557, 104560-104565, 104569, 104572, 104578, 104580, 104586, 104589, 104595, 104597, 104601, 104610, 104611, 104619, 104630, 104634, 104641, 104647, 104654, 104665, 104668, 104675, 104677, 104689, 104690, 104692, 104713, 104726, 104735, 104738, 104862, 116002, 116004, 116007, 116008, 123762, 138215; (SDSNH) 31929, 33096, 39296, 39301, 39302. SAN BERNARDINO: (LACM) 3018, 19919, 19921, 19922, 19924, 21908, 63632, 63634, 63643, 63645, 63647-63649, 70262, 70265, 70266, 70269, 104750, 104757, 104762, 104768, 104770, 104772, 104776, 104782, 104783, 104785, 104787, 104788, 104790-104793, 104796-104798, 116011, 116012, 125994, 132244; (SDSNH) 25397, 31758. SAN DIEGO: (LACM) 28002-28005, 76300, 104799, 104805, 104806, 104809, 104810, 104813, 125997, 126295.

RESULTS AND DISCUSSION

Testicular histology was similar to that reported by Goldberg & Parker (1975) for two colubrids *Masticophis taeniatus* and *Pituophis catenifer* (= *P. melanoleucus*) and the viperid *Agkistrodon piscivorus* by Johnson et al. (1982). In the regressed testis, seminiferous tubules

Table 1. Monthly distribution of reproductive conditions in seasonal testicular cycle of *Crotalus cerastes*. Values are the numbers of males exhibiting each of the three conditions.

Month	N	Regression	Recrudescence	Spermiogenesis
March	11	7	4	0
April	29	12	17	0
May	31	10	21	0
June	8	2	4	2
July	6	0	2	4
August	5	0	3	2
September	3	0	0	3
October	4	2	0	2

contained spermatogonia and Sertoli cells. There was a proliferation of germ cells; primary and secondary spermatocytes and occasional spermatids were present in testes undergoing recrudescence. During spermiogenesis, seminiferous tubules were lined by spermatozoa. Rows of metamorphosing spermatids were also present.

Monthly stages in the testicular cycle are shown in Table 1. Males undergoing spermiogenesis were present June to October; males with regressed testes were present in March-June and October. Reiserer (2001) found maximum testes sizes of *C. cerastes* occurred during September. Males with testes in recrudescence were present March to August. The presence of males undergoing spermiogenesis during summer and autumn indicates *C. cerastes* has a testicular cycle similar to those of other North American rattlesnakes in which sperm formation occurs during this period (Aldridge 1979b; Aldridge & Brown 1995; Goldberg 1999a, 1999b, 1999c, 2000a, 2000b, 2000c, 2002; Goldberg & Holycross 1999; Goldberg & Rosen 2000; Holycross & Goldberg 2001; Goldberg & Beaman 2003). This pattern of spermatogenesis fits the "aestival spermatogenesis" of Saint Girons (1982). Sperm were present in 74/75 (99%) of the vasa deferentia examined: March 8/9, April 27/27, May 21/21, June 3/3, July 4/4, August 4/4, September 3/3, October 4/4. The smallest mature male, LACM 104783 (regressed testis; sperm in vas deferens from previous spermiogenesis) measured 331 mm SVL (360 mm total length, TL). This is less than the smallest male (49.5 mm TL) found in copulation by Secor in Ernest (1992). Field observations have indicated *C. cerastes* mates both in spring (Klauber 1972; Brown & Lillywhite 1992) and fall (Lowe 1942).

Table 2. Monthly distribution of reproductive conditions in seasonal ovarian cycle of *Crotalus cerastes*. Values shown are the numbers of females exhibiting each of the four conditions.

Month	*n*	Inactive	Early yolk deposition	Enlarged follicles (> 8 mm width)	Oviductal eggs
January	1	0	1	0	0
February	1	1	0	0	0
March	1	1	0	0	0
April	10	3	4	3	0
May	30	9	1	20*	0
June	4	2	0	1	1
July	5	4	0	0	1
August	4	2	0	0	2
September	5	5	0	0	0
October	1	0	1	0	0

* Includes two females with damaged eggs; litters could not be reliably estimated.

Reiserer (2001) reported both spring and fall matings in captive *C. cerastes*. A captive pair of *C. cerastes* mated 11 October (Klauber 1972).

Mean female body size (SVL) was significantly larger than that of males ($t = 4.73$, $df = 157$, $P < 0.0001$). Reiserer (2001) similarly found female *C. cerastes* to be generally larger than the same-aged males. *Crotalus cerastes* may be the only species of North American *Crotalus* in which females are larger than males (Ernst 1992), however further study will be needed before this is known. Monthly stages in the ovarian cycle are shown in Table 2. Females with enlarged follicles (> 8 mm length) or oviductal eggs were present April to August. Reiserer (2001) reported ovulation in *C. cerastes* occurred during late June. The smallest reproductively active female (follicles > 8 mm length) (LACM 104549) measured 383 mm SVL (408 mm TL). This value is less than the 434 mm TL recorded for the smallest gravid *C. cerastes* female in Klauber (1944). There was no significant difference between the mean litter size (7.96 ± 2.9 *SD*, range = 3-14, $n = 26$) for *C. cerastes* in this study and the mean litter size in Klauber (1972) (9.5 ± 3.0 *SD*, range = 5-18, $n = 38$) $t = 2.0$, $df = 62$, $P = 0.05$. Litters may contain 1-20 young, but typically have 7-12 (Ernst & Ernst 2003). Fitch (1985), using data from Klauber (1972), reported mean litter sizes of 10.8 ± 0.1 SE, range: 7-18 for 10 *C. cerastes* from the Mohave Desert (northern) and 9.0 ± 0.5 SE, range: 5-16 for 28 from the Colorado

Table 3. Litter sizes for *Crotalus cerastes* from California.

Date	SVL (mm)	Litter size	County	LACM #
20 April 1961	485	7	Riverside	104552
27 April 1958	395	4	Riverside	104668
28 April 1962	560	4	Riverside	104738
3 May 1963	421	6	Riverside	104547
3 May 1963	451	6	Riverside	104578
4 May 1968	514	11	Riverside	116004
4 May 1968	528	9	Riverside	104713
5 May 1968	522	7	Kern	63644
5 May 1963	530	12	Riverside	28000
6 May 1961	522	13	Riverside	104619
7 May 1967	445	9	Los Angeles	52579
11 May 1974	435	11	Riverside	138215
16 May 1963	563	14	Kern	69905
16 May 1965	400	9	Riverside	104542
18 May 1966	509	9	Imperial	9203
19 May 1958	560	11	Riverside	104862
20 May 1961	435	7	Riverside	104630
20 May 1961	495	8	Riverside	104508
23 May 1958	438	5	Riverside	104595
24 May 1958	498	8	San Bernardino	104790
24 May 1963	383	3	Riverside	104549
12 June 1961	483	8	Riverside	104511
15 June 1960	463	8*	Riverside	104500
27 July 1962	490	3*	San Bernardino	21908
5 August 1968	498	6*	San Diego	125997
15 August 1954	459	9*	Riverside	3025

* Contained oviductal eggs; others contained enlarged follicles > 8 mm length.

Desert and Arizona (southern). There was no significant difference between mean litter sizes of these northern versus southern *C. cerastes* populations ($t = 1.7$, $df = 36$, $P = 0.10$). Examination of additional samples from other areas will be needed to ascertain the degree of geographic variation in *C. cerastes* litter sizes.

Litter sizes for 26 gravid *C. cerastes* females are given in Table 3. Regression analysis (Fig. 1) revealed a significant positive correlation between ln (litter size) and ln (SVL) for these 26 litters: (ln litter size =

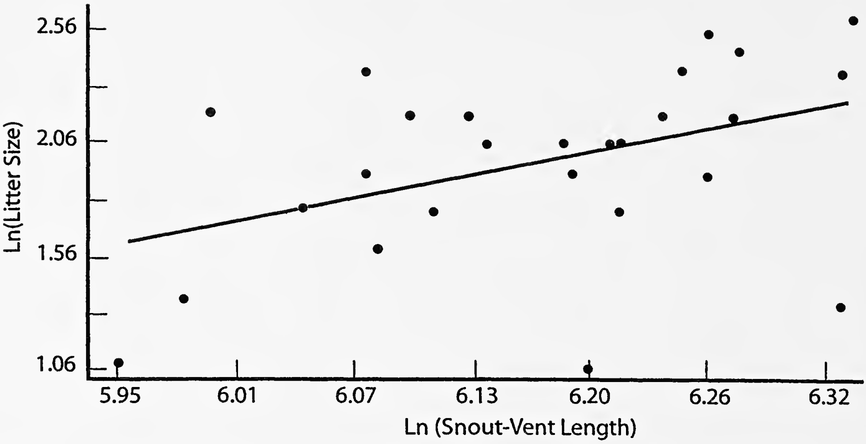

Figure 1. Linear regression of enlarged follicles (> 8 mm length) or oviductal eggs on snout-vent length, mm (log transformed variables) for 26 *Crotalus cerastes* females from California (regression equation in text).

-8.34 + 1.68 ln SVL) $r^2 = 0.19$, $P = 0.024$. Back transformed this regression equation describes the allometric relationship via a power function: litter size = $e^{-8.34}SVL^{1.68}$ (King 2000).

The number of gravid females (enlarged follicles > 8 mm or oviductal eggs) during the April to August period of female reproductive activity was 28/53 (53%). The presence of non-reproductive females (Table 2) during the period when other *C. cerastes* females are gravid indicates that not all females reproduce each year. This has been reported for other western North American rattlesnakes (Goldberg 1999a, 1999b, 1999c, 2000a, 2000b, 2000c, 2002; Goldberg & Holycross 1999; Goldberg & Rosen 2000; Holycross & Goldberg 2001; Rosen & Goldberg 2002). The frequency of reproduction in female rattlesnakes is unknown but is likely influenced by available food reserves (Goldberg & Rosen 2000; Rosen & Goldberg 2002). Long-term field studies will be required before the frequency of female reproduction can be known for *C. cerastes*.

The presence of *C. cerastes* females with early yolk deposition in April and May when other females were gravid (Table 2) suggests yolk deposition and ovulation are completed over more than one reproductive season and may be approximately biennial. Biennial reproduction may be "typical" for many species of North American rattlesnakes with the likelihood of less frequent reproduction during years of low food availability, and the potential of reproduction in successive years when food is abundant.

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FRESHWATER MUSSELS (BIVALVIA: UNIONIDAE) OF THE VILLAGE CREEK DRAINAGE BASIN IN SOUTHEAST TEXAS

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Abstract.—A total of 18 species and 2,235 individuals of freshwater mussels were collected from 22 sites in the Village Creek basin. The number of individuals per site ranged from zero to 528 and the number of species per site ranged from zero to 13. Relative abundance for all collection sites varied from zero to 176 individuals/person-hours. *Quadrula mortoni* and *Fusconaia askewi* comprised 60 percent of the total individuals collected and relative abundance was 14.8 and 13.1 individuals/person-hours, respectively. *Lampsilis satura, Obovaria jacksoniana* and *Pleurobema riddellii* were collected at several sites and are listed as "of special concern" by the American Fisheries Society.

Freshwater mussels are good indicators of water quality and are often the first organism to decline during adverse conditions (Rosenburg & Resh 1993; Howells et al. 1996; Howells 1997). Howells et al. (1997) reported that 52 species of freshwater bivalves occurred in Texas and discussed 18 that were dramatically reduced in abundance. Williams et al. (1993) listed 17 of these 52 species as threatened, endangered, or of special concern. This survey of the freshwater bivalves of the Village Creek drainage basin evaluates the current status of the populations and will serve as a baseline reference for subsequent studies.

There has been no extensive study of the bivalves of Village Creek. Strecker (1931) and Parks (1938) listed some bivalves that occurred in Village Creek, but these works are dated and uncertainties in systematics limit their present day use. Vidrine (1990) surveyed one location in Village Creek for his study of parasitic mites of freshwater mussels. Howells et al. (1996) listed some mussels known to have occurred in Village Creek, but in a later paper (Howells 1997) on the status of mussels in the Big Thicket region he mentioned an unsuccessful effort by Texas Parks and Wildlife Department personnel to collect any living mussels from Village Creek.

Several studies have been conducted on the physical/chemical conditions and macrobenthos of Village Creek and its tributaries (Tatum & Commander 1971; Harrel 1977; Kost 1977; Lewis & Harrel 1978;

Commander 1980; Newberry 1982; Harrel 1985; Barclay & Harrel 1985), but the sampling techniques were not adequate to survey the bivalve fauna. Nearby Texas and Louisiana mussel surveys were conducted by Neck (1986), Feaster (1997), Howells (2000) and Vidrine (2001).

DESCRIPTION OF THE AREA

Village Creek is a 5th order stream located in Hardin, Tyler and Polk counties in southeast Texas (Figure 1). From its origin, near the city of Livingston in Tyler County, it flows southeasterly into the Neches River. The basin drains an area of approximately 2,883 km^2 and has an axial length of 125 km. Land uses in the basin consist of lumber production, several small municipalities (< 10,000 residents) and scattered residential developments. Some reaches of Village Creek and its tributaries are within the boundaries of the Alabama-Coushatta Indian Reservation, the Big Thicket National Preserve, Roy Larsen Nature Conservancy Sanctuary and Village Creek State Park. The remaining sections of the stem stream of Village Creek, from the Big Thicket National Preserve Big Sandy Creek Unit to the confluence with the Neches River are proposed as additions to the Big Thicket National Preserve (Big Thicket National Preserve 1996).

The shallow substrate in the stream channel consisted of fine and coarse sand with pockets of silt, detritus and clay. Sunken logs are abundant. The average gradient is 0.38 m/km and the minimum and maximum daily discharge based on 66 years of record was 1.8 m^3/sec and 131.6 m^3/sec (USGS 2001). Dominant vegetation along the stream banks consists of *Taxodium distichum* (bald cypress), *Nyssa aquatica* (water tupelo), *Betula nigra* (river birch) and *Quercus* sp. (water tolerant oaks).

METHODS

Twenty-two sites were sampled between 9 August 2001 and 25 November 2002 (Figure 1). Seventeen sites were located along the lower stem stream and five sites were in smaller tributaries. Vidrine (1998) reported that small to moderate size streams resulted in low to moderate mussel diversity and larger, downstream reaches often had higher diversity and larger populations. At each site, 1.5 to 3 person-hours were spent hand-searching the substrate for mussels, covering an average of 50 meters of shoreline. Vaughn (1995) and Hornbach &

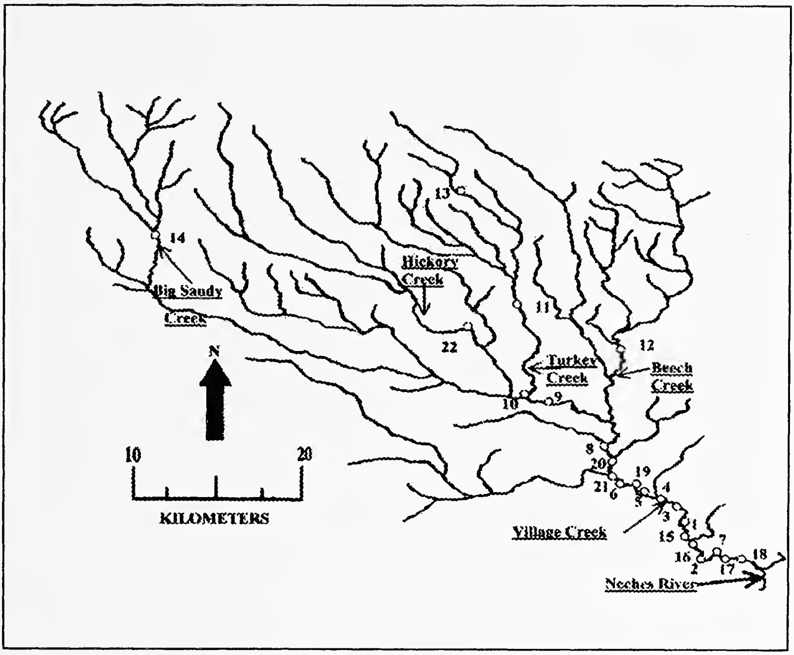

Figure 1. The Village Creek drainage basin and locations of sites sampled (in the order in which they were sampled).

Deneka (1996) stated that non-quantitative random time search methods are preferred when examining the distribution of freshwater mussels. Sampling was done only during relatively low stream discharge and depth conditions as indicated by the U.S.Geological Survey gauging station 08041500 located near Kountze, Texas (USGS 2001). Mean water depth for all collecting dates was 1.2 m and mean discharge was 5.6 m^3/sec. These conditions allowed productive sampling, which could not have occurred at greater depth or discharge.

Living mussels collected were identified, counted and measured. Most specimens were returned to the stream, but some were retained in order to confirm identification or to be used as reference specimens. Dead shell material was not documented. Retained specimens were returned to the laboratory and placed in three percent ethyl alcohol to cause the valves to gape, then preserved in 95 percent ethyl alcohol. Identifications were made using the following taxonomic references; Burch (1973), Cummings & Mayer (1992), McMahon (1991), Howells et al. (1996) and Vidrine (2001). Robert Howells (Texas Parks and

Table 1. Total number of living individuals of each species collected at each site sampled. (Total number of person-hours spent = 48.)

	Site										
	1	2	3	4	5	6	7	8	9	10	11
Amblema plicata	13	11	31	4	4	14	5	1	0	0	0
Fusconaia askewi	11	8	212	2	26	1	0	11	0	0	11
Fusconaia flava	2	3	12	0	5	0	0	5	0	0	6
Lampsilis hydiana	5	10	25	2	26	34	9	7	0	0	0
Lampsilis satura	4	3	0	0	0	0	0	0	0	0	0
Lampsilis teres	2	8	20	4	6	4	4	0	0	0	0
Leptodea fragilis	1	2	0	0	0	0	0	0	0	0	0
Obliquaria reflexa	0	0	0	3	1	1	0	1	0	0	0
Obovaria jacksoniana	0	6	0	4	3	0	0	0	0	0	0
Plectomerus dombeyanus	1	1	21	0	1	2	2	0	0	0	0
Pleurobema riddellii	1	5	1	0	0	0	0	0	0	0	0
Potamilus purpuratus	2	0	2	0	0	1	0	0	0	0	0
Quadrula mortoni	61	86	185	82	41	3	54	12	0	3	18
Quadrula nobilis	7	8	15	5	5	1	2	4	0	0	3
Toxolasma texasiensis	0	0	2	3	3	16	0	3	0	0	0
Tritogonia verrucosa	0	0	1	0	0	0	0	0	0	0	3
Uniomerus tetralasmus	0	0	0	0	0	0	0	0	0	0	0
Villosa lienosa	1	4	1	0	9	14	0	3	0	0	0
Total	111	152	528	109	130	91	76	47	0	3	41

Wildlife Department), verified the identifications. Common and scientific names are those of Turgeon et al. (1998).

Voucher specimens were placed in a collection at Lamar University. Relative abundance of all mussels for each collection site was calculated by the formula: number of individuals of all species collected/person-hours (48) spent collecting at that site. Relative abundance for each species was determined by the formula: number of individuals of a species collected/total person-hours (48) for entire study.

Table 1. (Continued)

	Site										
	12	13	14	15	16	17	18	19	20	21	22
Amblema plicata	0	0	7	9	25	4	6	8	15	5	4
Fusconia askewi	37	0	89	10	24	58	13	61	28	15	14
Fusconaia flava	6	0	7	2	16	3	4	3	2	5	0
Lampsilis hydiana	1	0	0	2	4	18	7	3	8	4	5
Lampsilis satura	0	0	0	17	2	3	0	1	0	3	0
Lampsilis teres	0	0	0	1	2	3	4	0	6	4	0
Leptodea fragilis	0	0	0	8	0	0	0	0	0	0	0
Obliquaria reflexa	0	0	0	0	0	0	0	0	0	1	0
Obovaria jacksoniana	0	0	0	0	0	0	0	3	0	0	0
Plectomerus dombeyanus	1	0	0	0	3	0	0	0	0	1	0
Pleurobema riddellii	0	0	2	0	2	0	0	0	0	0	0
Potamilus purpuratus	0	0	0	1	0	0	0	0	0	0	0
Quadrula mortoni	1	0	10	10	33	18	23	9	21	31	7
Quadrula nobilis	1	0	3	5	15	6	8	30	14	10	0
Toxolasma texasiensis	0	0	3	44	0	4	4	0	4	3	0
Tritogonia verrucosa	0	0	5	0	0	0	0	1	0	0	0
Uniomerus tetralasmus	1	1	0	0	0	0	0	0	0	0	0
Villosa lienosa	1	0	1	0	0	0	5	1	4	6	0
Total	49	1	128	109	126	117	74	120	106	88	30

RESULTS AND DISCUSSION

During the study, 18 species of unionds and 2,235 individuals were collected during a total of 48 person-hours (Table 1). The number of species per collection site ranged from zero at site 9 to 13 at sites 1, 2 and 3 (Table 2). The number of individuals per collection site ranged from zero (site 9) to 528 (site 3). No mussels were found at site 9 after 2.25 person-hours of searching. This was probably due to the unsuitable habitat that was composed of steep cut clay banks and tree roots, which made searching difficult. Relative abundance of all mussels at individual

Table 2. Number of species collected, mussels collected, person-hours spent collecting, and relative abundance for each collecting site. Data indicates living specimens only.

Site	Species collected	Number collected	Person-hours	Relative abundance
1	13	111	3	37
2	13	152	3	51
3	13	528	3	176
4	9	109	2	55
5	12	130	2	65
6	11	91	2.50	36
7	6	76	2	38
8	9	47	2	24
9	0	0	2.25	0
10	1	3	3	1
11	5	41	2	21
12	8	49	3	16
13	1	1	2.25	0.4
14	9	128	3	43
15	11	109	2	55
16	10	126	1.5	84
17	9	117	1.5	78
18	9	74	1.5	49
19	10	120	2	60
20	9	106	1.5	71
21	12	88	1.5	59
22	4	30	1.5	20

collection sites ranged from zero (site 9) to 176 (site 3) per person-hour (Table 2).

Site 3 had a large diversity of microhabitats including substrate types, variations in flow, and a large area of suitable depth for collecting. Site 3 is the location where Vidrine (1990) collected and removed 1,000 individuals for his study of mites associated with mussels. Site 3 is also the location where Texas Parks and Wildlife personnel reported finding no living mussels (Howells et al. 1996). This was probably due to their collecting method. They used a brail, which cannot be effectively utilized in Village Creek due to the amount of sunken trees.

Quadrula mortoni and *Fusconaia askewi* were the most abundant species, representing 31.8 and 28.2 percent, respectively, of the total number of individuals collected during the study (Table 3). Relative abundance of *Q. mortoni* and *F. askewi* was 14.8/person-hour and 13.1/person-hour, respectively. *Quadrula mortoni* occurred at 20 collecting sites and *F. askewi* occurred at 18 sites. These species are euryecious and were found in all types of substrates and were often the only species found in coarse sand away from the shore. One specimen

Table 3. Total number of sites where species occurred, total number of individuals collected, percentages of all individuals collected, and relative abundance of each species (in order of relative abundance). Data indicates living specimens only.

Species	Site frequency	Number collected	% of total collected	Relative abundance
Quadrula mortoni	20	712	31.8%	14.8
Fusconaia askewi	18	631	28.2%	13.1
Lampsilis hydiana	17	170	7.6%	3.5
Amblema plicata	17	166	7.4%	3.5
Quadrula nobilis	18	135	6.3%	2.9
Fusconaia flava	15	101	4.5%	1.7
Toxolasma texasiensis	11	89	4.0%	1.9
Lampsilis teres	13	68	3.0%	1.4
Villosa lienosa	12	50	2.2%	1.0
Lampsilis satura	7	33	1.4%	.7
Plectomerus dombeyanus	9	33	1.4%	.7
Obovaria jacksoniana	4	16	<1%	.3
Pleurobema riddellii	5	11	<1%	.2
Leptodea fragilis	3	11	<1%	.2
Tritogonia verrucosa	4	10	<1%	.2
Potamilus purpuratus	4	6	<1%	.1
Obliquaria reflexa	5	7	<1%	.1
Uniomerus tetralasmus	2	2	<1%	<.1

of *F. askewi* measured 74 mm in shell length, which exceeds the maximum length recorded for Texas waters (Howells et al. 1996). *Uniomerus tetralasmus* was the least abundant species and was collected only in two tributary streams; one specimen each in Beech Creek (site 12) and Turkey Creek (site 13). This species is adapted for desiccation, dewatering and stagnant water (Neck & Metcalf 1988; Cummings & Mayer 1992) and was the only species collected only in smaller tributary streams.

Three species found during this study are listed as of "special concern" by the American Fisheries Society (Williams et al. 1993). These include *Lampsilis satura, Obovaria jacksoniana* and *Pleurobema riddellii*. Only eight living specimens of *L. satura* had been reported in the Big Thicket region during the past five years (Howells 1997). During this study 33 specimens from seven sites were collected (Tables 1 & 3). Howells (1997) reported that only one dead shell of *Obovaria jacksoniana* had been found in Texas since 1990. During this study, 16 specimens of *O. jacksoniana* were collected from four sites (Tables 1 & 3). Since 1987, only two living and two dead specimens of *P. riddellii* have been reported from the central Neches River in Texas (Howells 1997). During this survey 11 specimens from four sites were collected (Tables 1 & 3).

Seven species of mussels were considered to be uncommon or rare and represented less than one percent of the total number collected and their relative abundance was less than 0.5 clams per person-hour (Table 3). Three species of mussels that were previously collected in Village Creek or the nearby Neches River during benthic surveys, but not during this study, include *Glebula rotundata, Quadrula apiculata* and *Megalonaias nervosa.* The exotic Asiatic clam, *Corbicula fluminea*, was noted at sites 1, 2, 4, 5, 8, 9, 11, 12, 13 and 20, but it was abundant only at sites 11 and 13 in Turkey Creek.

The results of this study indicate that Village Creek supports a diverse and healthy bivalve fauna. However, Neck (1982), Samad & Stanley (1986), Alderman & Adams (1993), Layzer & Gordon (1993) Neves (1993) and Howells (2000) reported that habitat alterations in and around waterways adversely alter mussel habitats. Within the basin, current and projected residential development and economic growth, together with increased recreational usage of Village Creek, may effect bivalve populations. The bivalve fauna should be monitored closely in the future to ensure protection of these organisms.

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GENERAL NOTES

NOTEWORTHY RECORDS OF THE MILLIPEDS, *EURYMERODESMUS ANGULARIS* AND *E. MUNDUS* (POLYDESMIDA: EURYMERODESMIDAE), FROM NORTHEASTERN AND WESTCENTRAL TEXAS

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The milliped family Eurymerodesmidae occurs from northeastern Nebraska, central Illinois and southeastern North Carolina to the Rio Grande and north Florida, and is the dominant representative of the order Polydesmida in the central United States (Shelley 1990). It is a monotypic genus, but is relatively diverse with 25 known species. *Eurymerodesmus mundus* Chamberlin has been reported from northeastern Nebraska through eastern Oklahoma and southwestern Arkansas to Cooke, Dallas, Grayson and Johnson counties, Texas, and *E. angularis* Causey is known from southern Missouri, the Coastal Plain of Arkansas, eastern Mississippi and northern Louisiana (Shelley 1990). This study provides the first report of *E. angularis* from Texas and four new records for *E. mundus* that significantly increase its known distribution within the state.

Between October 2001 and May 2003, locations (primarily in State Parks) within 24 Texas counties (Bosque, Bowie, Brown, Cass, Coryell, Dallas, Delta, Fannin, Freestone, Harrison, Hopkins, Jack, Johnson, Limestone, Marion, Morris, Parker, Red River, Shackleford, Somervell, Taylor, Titus, Tom Green and Travis) and Caddo Parish, Louisiana, were examined for millipeds in general and eurymerodesmids in particular. Individuals were encountered primarily in damp spots off park trails by overturning decaying logs and leaf litter with potato rakes. Occasional specimens were collected by peeling bark off fallen trees and rotting stumps. At each locale, specimens were placed in individually labeled vials containing 70% ethanol and returned to the laboratory for identification. Specimens were identified by examining the male genitalia. In eurymerodesmids both the gonopods and gonopodal apertures in males hold taxonomic utility as do the female cyphopods, which possess projections and other unique morphological features. Voucher specimens were deposited in the invertebrate collection of the North Carolina State Museum of Natural Sciences.

Several specimens of *E. mundus* were found during the study period in Texas; data are as follows:

Cass County, 8.1 mi (12.9 km) S Linden, along Yellow Poplar Trail off US Hwy. 59, 5♂, 3♀, 12 November 2001 and 26 November 2002. Dallas County, Cedar Hill State Park, DORBA and Talala Trails, 5♂, 4♀, 21 January and 16 November 2002. Morris County, Daingerfield State Park, Dogwood Camping Area, ♂, ♀, 26 November 2002. Taylor County, Abilene State Park, Elm Creek Nature Trail, 4♂, ♀, 17 November 2001. Titus County, Lake Bob Sandlin State Park, 3♂, 2♀, juv., 21 December 2002.

Eurymerodesmus mundus is readily recognized by the large, hirsute, clavate lobes on the caudal margin of the gonopodal aperture (Shelley 1990). Shelley speculated that the lobes must alter the millipeds' posture and locomotion because they are so disproportionately large in relation to the rest of the body that they would otherwise scrape the substrate or become impaled. The published record from Grayson County by Shelley was inadvertently omitted from the text; its data are Grayson County, Sherman, in storm cellar, 4♂, 7♀, 3 October 1967, M. Cundliff (Florida State Collection of Arthropods, Gainesville). The sites in Titus and Taylor counties are some 350 miles (563 km) apart, so *E. mundus* thus occupies the entire breadth of the family's distribution across northern Texas. The species also inhabits a variety of biotopes as habitats at these locales are quite different. The site in Cass County is a climax forest on acreage owned by International Paper Company that consists primarily of pines, yellow poplar and various oak species, while the sites in Morris and Titus counties are within state parks and comprised of mixed hardwoods. However, at the Dallas and Taylor County sites, the dominant trees are live oak, mesquite and eastern red cedar. In addition, the site in Dallas County includes trails situated near native tall grass prairie habitat. *Eurymerodesmus mundus* ranges northward to Nebraska, and in the "Ark-La-Tex" region (Fig. 1). Its occurrence in southwestern Arkansas (McAllister et al. 2002a) and northeastern Texas near the Louisiana state line suggest potential discovery in northwestern Louisiana (perhaps Bossier and/or Caddo parishes), which would constitute a new state record. Interestingly, a large female

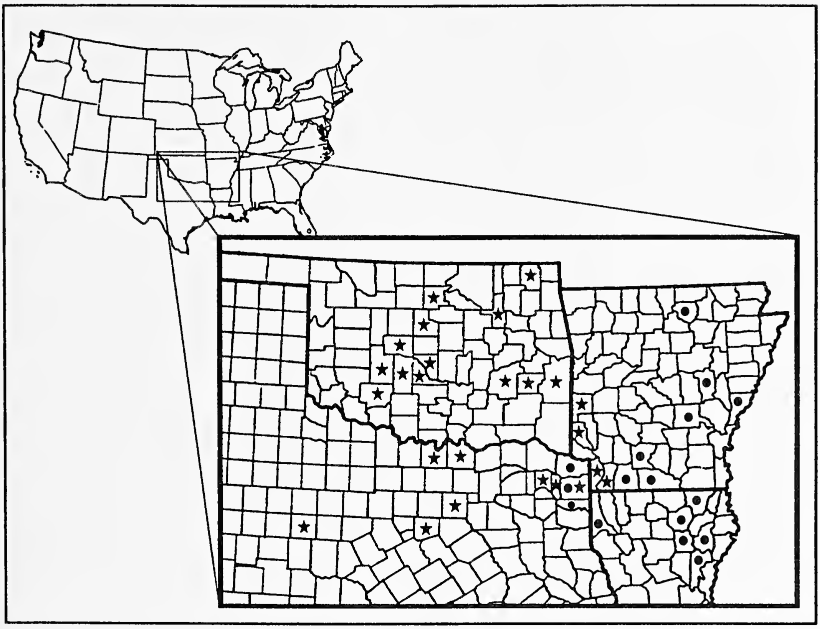

Figure 1. Map of the United States with inset of Arkansas and parts of Louisiana, Oklahoma and Texas showing county or parish distributions of *Eurymerodesmus angularis* (dots) and *E. mundus* (stars) within these states. County distributions of *E. mundus* in Kansas and Nebraska not included (see Shelley 1990).

Eurymerodesmus resembling *E. mundus* was collected by the senior author on 6 January 2003 in the vicinity of Oil City, Caddo Parish; however, an authentic male of *E. mundus* is necessary for specific identification.

Specimens of *E. angularis* were also encountered in three counties in the northeastern corner of Texas, confirming Shelley's prediction (1990) of discovery in this area. It represents a new species for Texas and the tenth species of *Eurymerodesmus* in the state. Data are as follows:

Bowie Co., 5 mi (8 km) W Texarkana, along County Road 1217 off FM 991, ♂, juv., 10 October 2001; S of Texarkana (Liberty Eylau) off FM 558 along County Road 1370, 10♂, 6♀, 11 October 2001 and 2♂, 19 December 2001; Texarkana, Texas A&M University campus off Robison Rd., 3♂, 5 November 2001. Cass Co., Atlanta, Ellington Clinic off U.S. Hwy. 59, 2♂, 7 November 2002. Marion Co., Jefferson, 2997 FM 728, Cypress Bend Adventist Elementary School, 3♂, 23 October 2002, and ♂, 4 mi (6.4 km) NW Jefferson, 9 November

2002. All specimens above represent new county records.

Habitat at these sites is typical east Texas pineywoods, and specimens were encountered while moving along the ground after brief fall showers. *Eurymerodesmus angularis* is a highly variable and widely ranging species (Fig. 1), and the most proximate prior record to this current study is that from the vicinity of Myrtis, ca. 30 miles (48.3 km) NNW Shreveport, Caddo Parish, Louisiana (Shelley 1990). Despite several efforts, no specimens of *E. angularis* were encountered in the vicinity of Caddo Lake State Park in adjacent Harrison County, but its presence is anticipated during the cooler and wetter months of fall and winter. Shelley (1990) depicted four gonopodal variants of *E. angularis* that he considered to be conspecific, and the northeast Texas form is that found in Caddo Parish, with lightly sinuate gonopodal acropodites and an aperture in which the caudolateral "pouch" flares strongly laterally.

To date little milliped sampling has taken place in northeast Texas (Stewart 1969). In addition, northeast Texas likely forms the western distribution boundary for a number of "eastern" diplopods and hence justifies more intensive investigation. Recent studies in proximate parts of Arkansas and Oklahoma produced several important discoveries (McAllister et al. 2002a; 2002b; 2003a; 2003b; Shelley et al. 2003), lending credence to this statement. Focused studies on the northeast corner of Texas may be similarly profitable and are a primary objective of future research.

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DIET OF THE WHITE-COLLARED SEEDEATER *SPOROPHILA TORQUEOLA* (PASSERIFORMES: EMBERIZIDAE) IN TEXAS

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The white-collared seedeater (*Sporophila torqueola)*, is a very small, black and white finch about 11 cm in total length. The species has a distribution from western Panama to the Rio Grande valley of Texas (American Ornithologists' Union 1998). *Sporophila torqueola sharpei* occurs from the Rio Grande of Texas, south along the coastal plain of northeastern Mexico to northern Veracruz, and west to eastern Nuevo Leon and San Luis Potosi (American Ornithologists' Union 1957). Most papers on temperate subspecies of *S. torqueola* are taxonomic, with virtually nothing written on its natural history, including diet (Eitniear 1997a). This paper summarizes dietary information collected in Texas from 1995-2000.

White-collared seedeaters were studied at two sites in Zapata County, Texas. Site 1 was located on the banks of the Rio Grande River within the city of San Ygnacio (27°02'N 99°26'W) in a black willow (*Salix niger*) dominated community, with an understory of barnyardgrass (*Echinochloa crus-pavonis*), Louisiana cupgrass (*Eriochloa punctata*), spreading panicum (*Panicum diffusum*), Bermudagrass (*Cynodon dactylon*) and Mexican sprangletop (*Leptochloa uninervia*).

Site 2, a marsh bordering a pond in Zapata County Park (26°54'N 099°16'W), was located within the city of Zapata. The habitat was characterized by Bermudagrass, buffelgrass (*Cenchrus ciliaris*), Guineagrass (*Panicum maximum*), Johnson grass (*Sorghum halepense)*, southwestern bristlegrass (*Setaria scheelei*), dock (*Rumex chrysocarpus*) and cattail (*Typha domingensis*). Trees included sugar hackberry (*Celtis laevigata*), black willow, huisache (*Acacia minuata*) and guajillo (*Acacia berlandieri*). Plant identifications follow that of Hatch et al. (1990).

METHODS AND MATERIALS

Observations were made from April to August 1995 at Site 1 (Eitniear & Rueckle 1995) and August to October 1994, February 1996, April 1997 and April 2000 at Site 2. Observations began at either 0800 h or 1000 h and continued to about 1800 h or 1900 h. Five birds were captured in mist-nets set at the site. Captured birds were leg banded and placed in a holding cage until a fecal sample was caught on blotting paper placed at the bottom of a small field cage. It was assumed these bird's fecal contents, although biased by a digestive differential of certain foods, provided a representative sample of recently consumed foods. The white uric acid covering was removed by flushing the sample with water. The remaining fecal mass was stored in 70% ethanol. Food items were identified by comparison to a reference collection of seeds and leaves from all plants at the study sites (Smith 1970; Servat 1993). Observations of foraging birds were conducted using 10 by 50 binoculars. Foraging observations were documented in a field notebook and a botanical specimen, from plants that contained seeds fed on, collected. Plant specimens were later identified by Robert Lonard (UT-Pan American). On occasion seeds were obtained from the mouths of captured birds. No effort, however, was made to flush crops.

RESULTS AND DISCUSSION

Items in the diet of the species are summarized in Table 1. The largest foraging group of seedeaters observed consisted of approximately 10 birds feeding on barnyardgrass and Louisiana cupgrass at Site 1. The birds fed throughout the day, frequently retreating to nearby black willows. Females were observed feeding Louisiana cupgrass seeds to recently fledged young at this location (Eitniear & Rueckle 1995). Fecal samples (five samples from five different birds) contained only barnyard and Louisiana cupgrass seeds, thus supporting the theory that grasses were the principle food resource consumed at this time. Green Louisi-

Table 1. Parts of 12 plants consumed by *Sporophila torqueola sharpei* in Zapata, Zapata County, Texas, 1995-2000.

Plant Species	Part
Eriochloa cruz-pavornis	(seeds)
*Panicum maximum**	(seeds)
Echinochloa punctata	(seeds)
Panicum diffusum	(seeds)
*Dichanthium annulafusum**	(seeds)
*Panicum antidotale**	(seeds)
*Cenchrus cilaris**	(seeds)
Setaria leucopila	(seeds)
Setaria scheelei	(seeds)
Acacia minuata	(floral parts)
Salix nigra	(floral parts)
Salix exigua	(floral parts)

*Non-native species

ana cupgrass seeds in the milky stage of development were collected from the mouth and outer portions of the mandible of a female caught in a mist net. Plant succession altered this site significantly during the study. Black willow displaced barnyardgrass along the riverbank, and plains bristlegrass, buffelgrass, Guineagrass and blue panicum became established in open areas.

Seedeaters at Site 2 were observed feeding on southwestern bristlegrass, barnyardgrass and Louisiana cupgrass. Bermudagrass, Guineagrass, Johnsongrass and buffelgrass also were abundant, and contained ripe seeds, but not observed to be utilized as a food resource. Although grass seeds dominated observations of white-collared seedeaters diet, at 1200 h on 25 February 1996 at Site 1, a male foraged on huisache blossoms in a tree near the pond. For 30 minutes it was observed consuming the orange globose clusters of stamens. Subsequent to this observation, seedeaters had been observed feeding on the floral parts of willow (Table 1).

Bill morphology of the genus *Sporophila* favors seed eating (Cody 1985). Observations made during this study, although somewhat limited, support this concept. The greater proportion of barnyardgrass in the diet of the white-collared seedeater may reflect the greater abundance of this species over cupgrass and southwestern bristlegrass at Site 2 (Eitniear 1997b). Despite barnyardgrass growing abundantly on the opposite side of the pond at Site 2, seedeaters were never observed feeding on it; perhaps because no cover existed nearby.

Observations of feeding on the floral parts of willow and huisache in addition to records of its feeding on berries in Costa Rica (Stiles & Skutch 1989) and the pulp of *Stemmadenia donnell-smithii* in Mexico (McMiarmid et al. 1977) indicates greater plasticity in diet than previous authors have indicated (Cody 1985; Rubenstein et al. 1977). More research is needed to determine dietary shifts in this species in relation to changing seasons, variations in precipitation levels and landscapes. Such research may indicate if the decline of this species from a formerly robust widespread species in south Texas to the current patchily distributed remnant population is principally the result of the use of agrochemicals, habitat loss or some other factors (Eitniear & Rueckle 1996; Woodin et al. 1999).

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REPRODUCTION IN THE COFFEE SNAKE, *NINIA MACULATA* (SERPENTES: COLUBRIDAE), FROM COSTA RICA

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The coffee snake, *Ninia maculata* is known from Honduras, Nicaragua, Costa Rica and Panama from 36-1800 m (Savage 2002). Fitch (1970) reported *N. maculata* clutch sizes from Cartago Province, Costa Rica. The purpose of this paper is to provide new information on the reproductive cycle from a histological examination of gonads and kidneys and additional data on clutch sizes.

A sample of 41 specimens of *N. maculata* from Costa Rica (females n = 25, mean snout-vent length [SVL] = 226 mm ± 22 *SD*, range = 175-275 mm; males n = 16, SVL = 201 mm ± 15 *SD*, range = 179-228 mm) was examined from the herpetology collection of the Natural History Museum of Los Angeles County, Los Angeles (LACM). Snakes were collected 1959-1996. Counts were made of enlarged ovarian follicles (> 8 mm length) or oviductal eggs. The left testis, vas deferens and a portion of the kidney were removed from males and the left ovary was removed from females for histological examination. Tissues were embedded in paraffin and sectioned at 5 μm. Slides were stained with Harris' hematoxylin followed by eosin counterstain. Histological slides were examined to determine the stage of the testicular cycle and for the presence of yolk deposition (secondary vitellogenesis *sensu* Aldridge 1979). Not all tissues were available for histological examination due to damage or autolysis. Number of tissues histologi-

Table 1. Monthly distribution of stages in the ovarian cycle of *Ninia maculata* from Costa Rica. Values shown are the numbers of females exhibiting each of the four conditions.

Month	*n*	Inactive	Early yolk deposition	Enlarged follicles > 12 mm length	Oviductal eggs
February	2	1	0	0	1
June	3	2	0	0	1
July	3	2	0	0	1
August	4	0	1	1	2
September	4	2	0	2	0
October	1	0	0	1	0
November	8	1	2	3	2

Table 2. Clutch sizes for *Ninia maculata* (estimated from counts of yolked follicles > 8 mm length or oviductal eggs*) from Costa Rica.

Date	SVL (mm)	Clutch size	Province	LACM #
11 February	240	3*	Cartago	153798
29 June	230	3*	Limón	153808
11 July	215	2*	Cartago	153828
2-6 August	220	2*	Guanacaste	153788
27 August	210	3*	San José	153857
30 August	220	3	San José	153843
15 September	225	4	San José	153851
16 September	246	4	Cartago	153802
13 October	213	2	San José	153831
10 November	190	1	San José	153849
14 November	225	2	San José	153856
20 November	223	3*	San José	153823
20 November	240	5	San José	153821
22 November	233	4	San José	153835

cally examined by specimen were: testis = 16, vas deferens = 3, kidney = 13, ovary = 11. Follicles in advanced stages of yolk deposition or oviductal eggs were counted, but were not examined histologically. An unpaired *t*-test was used to compare body sizes of male and female samples. The relationship between female SVL and clutch size was examined by linear regression analysis.

Material examined.—The following specimens of *Ninia maculata* were examined by Costa Rica province: CARTAGO (LACM 153787, 153795, 153798, 153799, 153801-153805, 153828), GUANACASTE (LACM 153788, 153789), LIMÓN (LACM 153807, 153808, 153812), PUNTARENAS (LACM 153790), SAN JOSÉ (LACM 38063, 38064, 153818, 153819, 153821, 153823, 153824, 153826, 153829, 153831, 153834, 153835, 153839, 153840, 153843, 153844, 153846, 153848-153852, 153856-153858).

Testicular histology of *N. maculata* was similar to that reported by Goldberg & Parker (1975) for two colubrid snakes, *Masticophis*

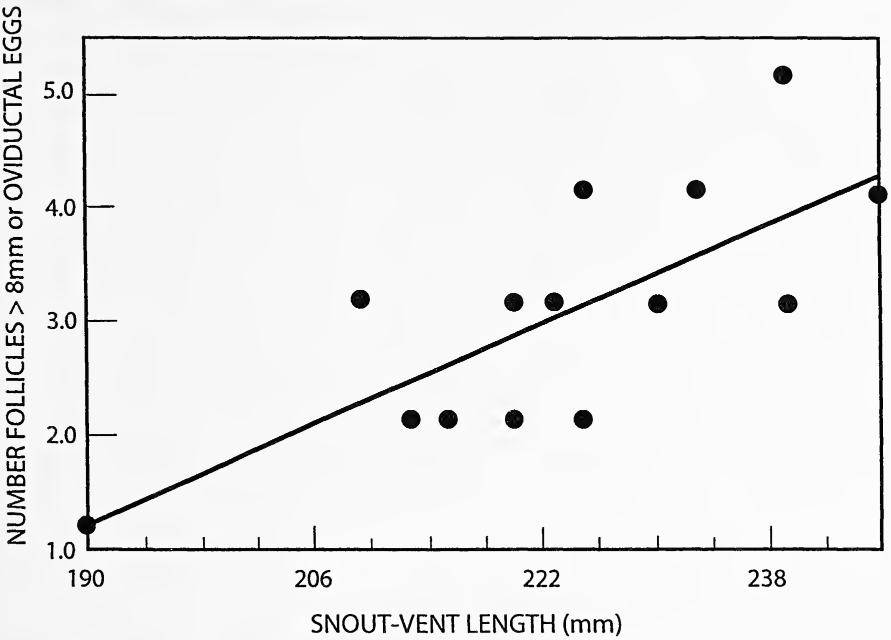

Figure 1. Linear regression of female body size (mm) versus clutch size for fourteen *Ninia maculata* from Costa Rica.

taeniatus and *Pituophis catenifer*. All testes examined exhibited spermiogenesis with metamorphosing spermatids and sperm present. The following numbers of males were undergoing spermiogenesis by month: February (3), April (1), June (3), July (2), August (2), September (1), October (2), November (2). All three vasa deferentia examined contained sperm: April (1), July (1), November (1). All thirteen kidney sexual segments examined were enlarged and contained secretory granules: February (2), April (1), June (2), July (2), August (1), September (1), October (2), November (2). Mating usually coincides with enlargement of the kidney sexual segments (Saint Girons 1982). The smallest spermiogenic males measured 179 mm SVL (LACM 153805, 153858). Males smaller than this size were not examined, therefore the minimum size at which *N. maculata* begins sperm formation is unknown.

Females were significantly larger than males (unpaired *t*-test, $t = 4.01$, $df = 39$, $P < 0.001$). Females with enlarged follicles (> 8 mm length) or oviductal eggs were observed February, June-November (Table 1). The smallest reproductively active *N. maculata* female (one oviductal egg) measured 190 mm SVL (Table 2), while the three females undergoing early yolk deposition measured 207 mm SVL (14 November, LACM 153818), 240 mm SVL (27 August, LACM 153850), 246 mm SVL (22 November, LACM 153852). The minimum size at which *N. maculata* females commence reproduction remains to be determined. There was no evidence that females produce more than one clutch of eggs in a reproductive season (i.e., oviductal eggs and yolk deposition in progress in the same female) although the presence of reproductively active females during seven months of the year (Table 2) suggests this might be possible. Fitch (1970) reported gravid female *N. maculata* from Volcán Turrialba, Cartago Province, Costa Rica that measured 187, 206, 218, 222, 231 and 233 mm SVL respectively. A dissected female contained five eggs. One female was collected 2 June and three were collected 30 August.

All clutch sizes are listed in Table 2. Mean clutch size for 14 egg clutches from Costa Rica was 2.9 ± 1.1 *SD*, range = 1-5. Linear regression analysis revealed a significant positive correlation between female body size and clutch size $Y = -9.87 + 0.06X$, $r = 0.77$, $P = 0.001$ (Fig. 1).

The preceding observations on the ovarian cycle and the presence of males undergoing spermiogenesis during eight months of the year suggests that *N. maculata* has a prolonged reproductive cycle. Fitch (1970) similarly concluded that *N. maculata* reproduced throughout much of the year in Costa Rica, if not all of it.

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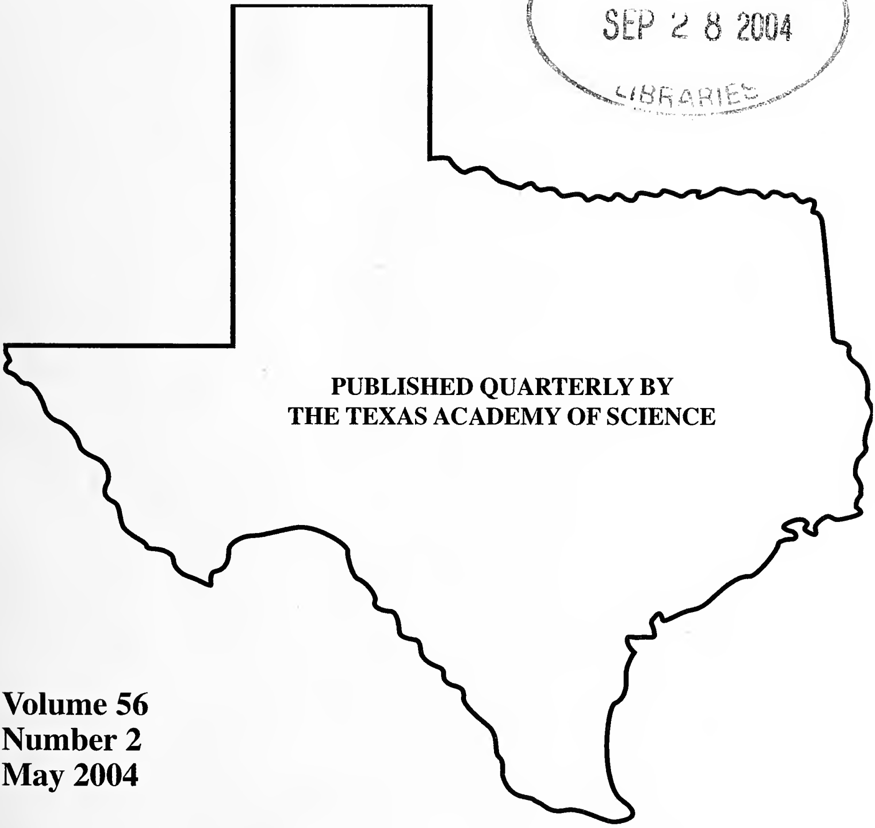

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CONTENTS

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NATURAL SOURCE OF ARSENIC IN EAST TEXAS LAKE SEDIMENTS

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Abstract.—Elevated arsenic levels occur in the sediment of several east Texas reservoirs. Eight reservoirs exceed the statewide 85th percentile of 17 mg/kg dry weight for arsenic in lake sediment. Average arsenic concentrations in the sediments of these lakes ranges from 19.5 - 83.5 mg/kg. The source of the arsenic is the marine mudstone formations which crop out in east Texas. Arsenic is common in marine mudstone where it substitutes for sulfur in the mineral pyrite. Unusually high levels of arsenic (up to 122 mg/kg compared to a global average of 13 mg/kg) are known to occur in the Weches Formation in east Texas. Other east Texas marine mudstone formations have not been analyzed for arsenic content. Oxidation of arsenic-bearing pyrite produces acid sulfate conditions, precipitated $Fe(OH)_3$ and oxidized arsenic species. Arsenic species readily adsorb to $Fe(OH)_3$ which is transported to reservoirs by streams and incorporated into the sediment.

Arsenic has recently been found to occur at elevated levels in some east Texas rock units (Ledger & Judy 2003). It probably substitutes for sulfur in the ubiquitous mineral pyrite. Pyrite occurs in a variety of geologic settings, including marine mudstone formations in which iron and sulfur were both present and conditions were sufficiently anaerobic to reduce them. This type of depositional environment was present at times in east Texas during the Eocene. Present day exposure of pyrite-bearing mudstone formations to oxygenated surface and ground water oxidizes the pyrite and releases arsenic into the environment. Monitoring of streams and lakes by the Texas Commission on Environmental Quality (TCEQ) generally shows levels of arsenic in lake water well below the MCL (Maximum Contaminant Level) established by the EPA. However, elevated arsenic levels occur in the sediment of several east Texas reservoirs.

GEOLOGIC SETTING

The Claiborne Group consists of a thick series of cyclic transgressive/regressive sedimentary strata deposited in east Texas during the middle Eocene (Deussen 1911; Dumble 1918; Berg 1970; Collins 1980; Collins 1982). The Queen City Sand, Sparta Sand, Carrizo Sand and Yegua Formations are composed of fine to medium grained sand deposited in a nearshore environment. The Reklaw Formation, Weches Formation and Cook Mountain Formation are composed primarily of mudstone deposited in a quiet marine environment such as a lagoon or shelf (Figure 1).

There are few data available, but the pyrite content of the mudstone formations appears to vary laterally and can be appreciable. Selected hand specimens from the southern part of the Weches Formation contain as much as 10% pyrite with some crystals being up to a few millimeters in diameter. Further north, pyrite is rare, while siderite ($FeCO_3$) is abundant.

The arsenic content is virtually unknown, but likely to be high where pyrite is abundant. Eight samples from a road cut near Nacogdoches, Texas average almost 100 mg/kg arsenic (Ledger & Judy 2003) compared to a global average shale value of 13 mg/kg.

Present day weathering of the mudstones occurs most rapidly where the formations crop out or are near the surface. This process releases soluble arsenic oxides into ground and surface water. Past structural events have affected the outcrop patterns, stream patterns, and even the deposition of east Texas rock units. Most of the rock layers in the eastern half of Texas dip gently to the southeast, toward the Gulf of Mexico. However, the dip rate flattens out and then reverses to northwest or west dip on the Texas side of the Sabine Uplift, a circular regional structure located in northeast Texas and northwest Louisiana over a basement high (Nicolas & Waddell 1989). An uplift is an area where deep rocks have been pushed upward. The zone of flat to reversed dip on the flank of the Sabine Uplift causes the Weches, and other possibly arsenic bearing formations, to have a much wider outcrop area than they would have otherwise. Jackson & Laubach (1991) concluded that the Sabine area was uplifted about 170m during the middle of the Cretaceous, and that a second episode of uplift occurred early in the Eocene.

Three major fault systems also affect east Texas rock outcrops: the Mt. Enterprise, Mexia and Talco fault zones. These fault systems consist of down-dropped grabens bounded by normal faults which formed when overloading of sedimentary rock deposits above the unstable low-density Louann Salt caused the salt to flow and intrude upward into areas of lesser pressure (Jackson & Wilson 1982). The Mt.

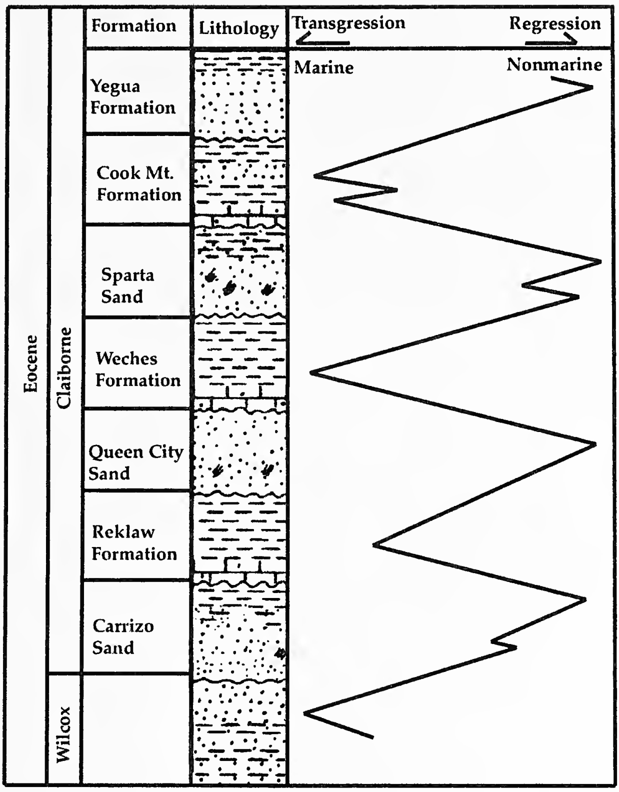

Figure 1. Stratigraphic column of the Middle Eocene Claiborne Group of east Texas (modified from Satin & Brooks 1977).

Enterprise fault system is a linear zone of grabens trending east northeast that are bounded by growth faults that were active during the time of sediment deposition (Ferguson 1984). Structural control of stream drainage patterns shows up on detailed maps as stream segments aligned with faults and grabens (Baumgardner 1987). Fault and joint fracture planes are primary conduits for movement of ground water through otherwise impermeable mudstone layers and thus may exert significant control on the localization of arsenic, iron and other elements.

RESULTS OF WEATHERING

Oxidation of pyrite produces Fe(III) and acid sulfate conditions. Fe(III) is mobile below about pH 3-4. At higher pH, Fe(III) quickly hydrolyzes to precipitate as amorphous $Fe(OH)_3$, a red, colloidal gel.

This is easily transported by streams as suspended or bed load and settles out in calmer lake settings.

Initial breakdown of pyrite underground:

$$2FeS_2 + 2H_2O + 7O_2 => 2Fe^{2+} + 4SO_4^{2-} + 4H^+$$

Oxidation and hydrolysis of Fe^{2+} in contact with atmosphere:

$$4Fe^{2+} + O_2 + 10H_2O => 4Fe(OH)_3 + 8H^+$$

Under strong oxidizing conditions, As(V) is thermodynamically stable, but the As(III)/As(V) transformation occurs at such a slow rate that both species are usually present. $H_2AsO_3^-$ and $H_2AsO_4^-$ are the most abundant species in well oxygenated surface water between pH 3-7. Arsenic species readily adsorb to Fe-oxides and clay minerals and become incorporated in the sediment of streams and lakes.

RATES OF WEATHERING

The rate at which pyrite oxidizes in natural environmental systems is usually accelerated by the action of sulfur and iron oxidizing bacteria such as *Thiobacillus* sp., *Ferrobacillus* sp., *Gallionella*, *Sphaerotilus* and others (Langmuir 1997). Rates of oxidation caused by bacterial catalysis vary greatly depending on pH, surface area of pyrite, dissolved oxygen concentration and other factors. However, the rate increase is commonly in orders of magnitude (Olson 1991; Stumm & Morgan 1996; Edwards et. al. 1998).

Such rapid oxidation results in pH levels low enough that $Fe(OH)_3$ does not form and arsenic species are mobile in ground or surface waters. Judy (1999) measured pH as low as 3.95 in distilled water mixed with dried samples of the Reklaw formation.

SCREENING LEVELS FOR ARSENIC

Currently, no federal or state standards for allowable levels of arsenic in lake sediments exist. The National Oceanic and Atmospheric Administration (NOAA 1999) has established probable effects levels (PELs) for substances at which they are likely to be toxic. For arsenic in lake sediment, the PEL is 32.7 mg/kg. To identify water bodies with elevated sediment metals concentrations, the TCEQ uses a statewide 85th percentile. These are derived from long-term monitoring data and indicate concentrations below which 85% of measurements occur. State-

Table 1. Average concentration of arsenic in sediment (mg/kg) for twenty-one lakes in east Texas (data provided by the TCEQ, 1985-003).

Reservoir	Average Concentration of Arsenic in Sediment (mg/kg)	Number of Samples
Lake Nacogdoches	83.5	2
Lake Jacksonville	53.8	4
Sam Rayburn Reservoir	34.1	22
Lake Cherokee	31.0	2
Ellison Creek Reservoir	30.3	7
Pinkston Reservoir	28.0	1
Lake Tyler East	24.1	4
Lake Tyler	20.0	4
Lake Palestine	10.3	6
Lake O' the Pines	8.9	6
Martin Lake	8.8	3
Caddo Lake	8.7	6
Wright Patman Lake	6.1	10
Lake Monticello	5.8	4
Houston County Lake	5.8	1
Lake Bob Sandlin	5.3	13
Lake Cypress Springs	4.2	16
Toledo Bend Reservoir	3.3	9
Lake Fork Reservoir	2.7	5
Lake Murvaul	2.5	2
Lake Tawakoni	1.7	3

wide 85th percentiles indicate areas where metals concentrations are elevated and are not based on negative biological effects. For arsenic in sediment in reservoirs, the statewide 85th percentile is 17 mg/kg, close to the global average of 13 ppm for shale.

METHODS

All data for arsenic levels in lake sediments were provided by the Texas Commission on Environmental Quality (TCEQ) and are available to the public. If available, data collected between 1 January 2000 and 1 April 2003 were used. Some lakes were not monitored for arsenic in sediment during this time period. For these, data acquired between 1985 and 2000 were used.

Surface outcrops of the Weches Formation, Reklaw Formation and Cook Mountain Formation are those shown on the Geologic Atlas of Texas Texarkana Sheet (Barnes 1979), Palestine Sheet (Barnes 1993) and Tyler Sheet (Barnes 1975). Stream drainage patterns were illustrated based on the Geologic Atlas of Texas and USGS topographic maps.

RESULTS AND DISCUSSION

In general, lakes receiving substantial discharge from streams flowing through mudstone formations have elevated levels of arsenic in their sediments. Eight of the twenty-one lakes for which arsenic in sediment data are available exceed the statewide 85th percentile of 17 mg/kg and three exceed the PEL of 32.7 mg/kg (Table 1). Four of these: Lake Nacogdoches (Figure 2), Lake Jacksonville (Figure 3), Lake Tyler (Figure 4) and Ellison Creek Reservoir (Figure 5) are near outcrops of the Weches Formation and are fed by streams which flow through it. Lake Cherokee (Figure 6) is fed by discharge from streams flowing through outcrops of the Reklaw Formation which may contain elevated arsenic levels. Sam Rayburn Reservoir (Figure 7) is fed by large streams which flow across the Weches, Reklaw and Cook Mountain Formations. Lake Tyler East (Figure 4) and Pinkston Reservoir have elevated sediment arsenic levels but do not have a source that is apparent on the geologic map.

The remaining thirteen lakes are all well below the statewide 85th percentile. Ten of these are fed by streams which flow primarily across sand formations. The remaining three: Lake Palestine (Figure 8); Lake O' the Pines (Figure 5); and Houston County Lake receive some stream drainage from mudstone outcrops, but do not show elevated levels of arsenic in their sediment.

Individual study of the five lakes which appear to be anomalous is likely to reveal a simple explanation for the levels of arsenic present. For example, Lake O' the Pines (Figure 5) is near the northern Weches in which siderite formed and pyrite is rare. Field research by the authors found that surface outcrops in this area are very thin, only a few feet in some locations. Also, small reservoirs are present on the two major streams flowing across the Weches Formation into Lake O' the Pines. These would trap sediment before it gets to the lake. Therefore, it is seems that arsenic is either not present, not abundant, or is being trapped in the smaller reservoirs.

The proximity of a reservoir to mudstone outcrops is not a perfect predictor of elevated arsenic levels in lake sediments. However, the correlation observed here suggests that this would be useful in deciding which lakes to most closely monitor.

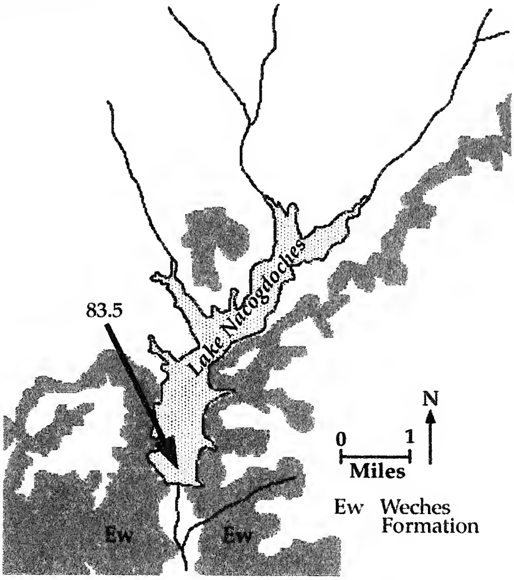

Figure 2. Lake Nacogdoches, Texas. Arsenic-bearing formation outcrop is shown in dark gray. Arrow with number indicates average concentration of arsenic in sediments in mg/kg dry weight at sampling sites.

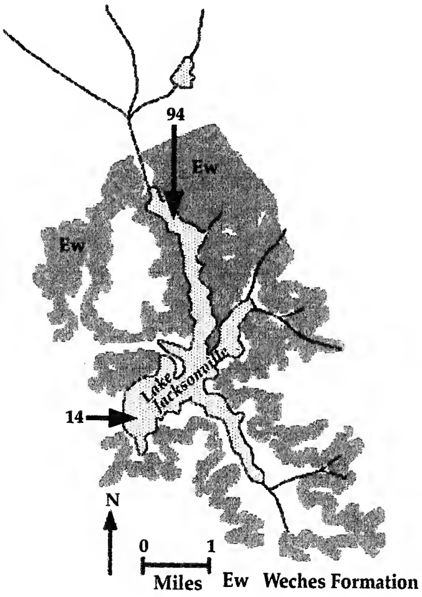

Figure 3. Lake Jacksonville, Texas. Arsenic-bearing formation outcrop is shown in dark gray. Arrows with numbers indicate average concentrations of arsenic in sediments in mg/kg dry weight at sampling sites.

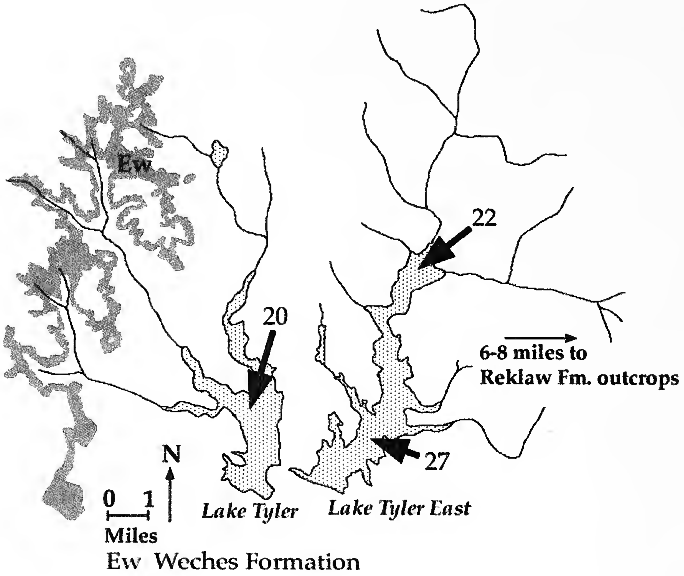

Figure 4. Lake Tyler and Lake Tyler East, Texas. Arsenic-bearing formation outcrop is shown in dark gray. Arrows with numbers indicate average concentrations of arsenic in sediments in mg/kg dry weight at sampling sites.

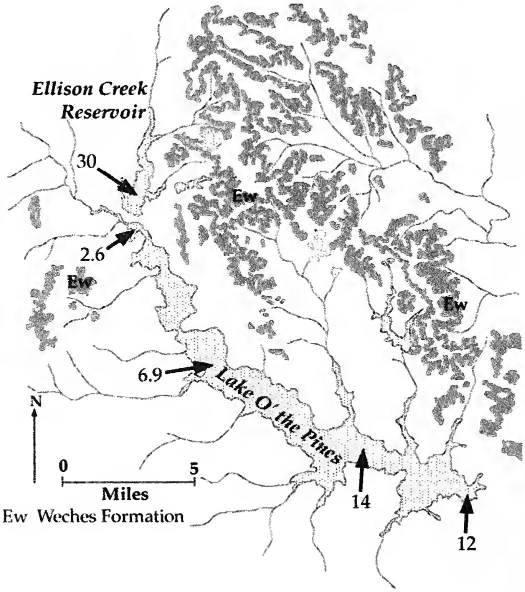

Figure 5. Ellison Creek Reservoir and Lake O' the Pines, Texas. Arsenic-bearing formation outcrop is shown in dark gray. Arrows with numbers indicate average concentrations of arsenic in sediments in mg/kg dry weight at sampling sites.

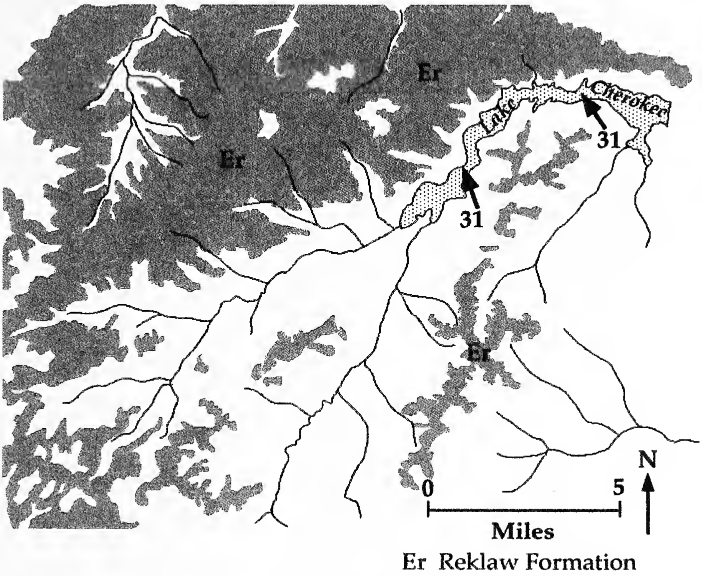

Figure 6. Lake Cherokee, Texas. Arsenic-bearing formation outcrop is shown in dark gray. Arrows with numbers indicate average concentrations of arsenic in sediments in mg/kg dry weight at sampling sites.

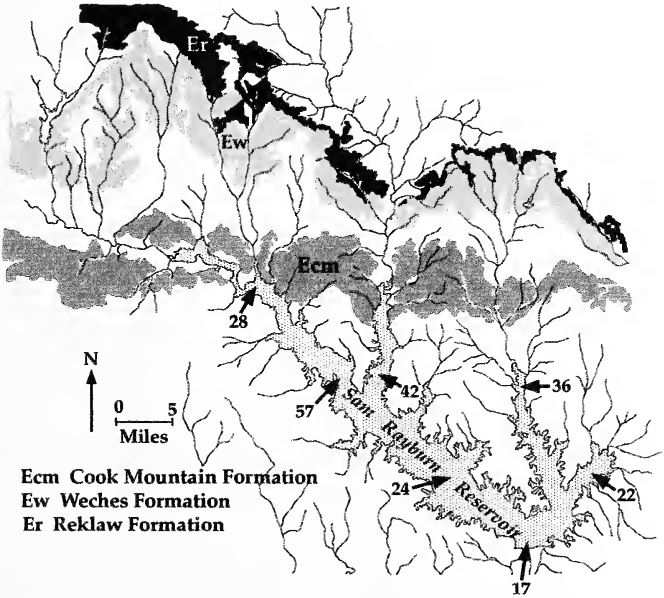

Figure 7. Sam Rayburn Reservoir, Texas. Arsenic-bearing formation outcrop is shown in dark gray. Arrows with numbers indicate average concentrations of arsenic in sediments in mg/kg dry weight at sampling sites.

Figure 8. Lake Palestine, Texas. Arsenic-bearing formation outcrop is shown in dark gray. Arrows with numbers indicate average concentrations of arsenic in sediments in mg/kg dry weight at sampling sites.

Arsenic in lake sediments is not bioavailable to pelagic organisms or organisms that drink the lake water. Its possible effects on benthic organisms may be a field of future study. An interesting and unanswered question is whether or not arsenic is bioavailable at any time between the initial weathering of arsenic-bearing pyrite and the deposition of $Fe(OH)_3$ with adsorbed arsenic species.

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COMMUNITY ECOLOGY OF FRESHWATER, BRACKISH AND SALT MARSHES OF THE RIO GRANDE DELTA

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Abstract.—Species composition and importance, species diversity and evenness, species richness, and community similarity are compared among 6 freshwater, 9 brackish and 11 salt marshes in the Rio Grande Delta. Community similarity is generally low among marshes, but salt marshes have a greater mean coefficient of similarity than brackish marshes. Species richness per marsh ranges from 15 to 31 for freshwater marshes, 7 to 24 for brackish marshes and 7 to 26 for salt marshes. Each freshwater marsh has a different dominant species. The first six species in importance in all three kinds of marshes contribute from 72.6 to 99.8% of the relative cover. Thus, most species are of low importance. There is no significant difference in species richness, species diversity or evenness among the three kinds of marshes. The generalization of the relationships found in this study awaits additional information on marshes from other areas of the Texas coast.

The physiography of southern Texas is characterized by offshore barrier islands, an enclosed lagoon (Laguna Madre), and the delta of the Rio Grande on the Texas mainland. The base of the delta is about 46 km long extending from Port Mansfield in Willacy County to the mouth of the Rio Grande in Cameron County. The apex of the delta is located approximately 66 km inland from the Gulf of Mexico (Brown et al. 1980).

Prior to the construction of dams, floodways and levees, the Rio Grande overflowed its banks annually depositing new sediment and moving water into a variety of meander channels in the delta. These floodwaters constituted significant freshwater input into the wetlands of the Rio Grande Delta. However, in the past 50 years dams and flood control projects have eliminated this source of freshwater (Jahrsdoerfer & Leslie 1988) and the wetlands are now dependent on rainfall alone for freshwater input.

Unlike streams of the upper and central Texas coast, the Rio Grande does not have associated swamps or freshwater marshes (White et al. 1986). Rather, there is a gradational array of infrequently to permanently inundated wetlands in the Rio Grande Delta. Brackish marshes are common because: (1) evaporation exceeds precipitation, (2) prevailing southeasterly winds carry salt spray inland from the Laguna Madre and, (3) extremely high storm tides flow inland along drainage courses during hurricanes (Brown et al. 1980). Salt marshes are less common and less extensive because wind-tidal flats occupy the areas of the delta that are typically occupied by salt marshes on the central and upper Texas Coast (Brown et al. 1980). Freshwater marshes are even more uncommon because of the absence of freshwater input by river overflow and low annual rainfall.

Little information is available on the marshes of the Rio Grande Delta. White et al. (1986) used color-infrared photographs to identify and classify wetlands in the delta. They recognized seven major kinds of wetlands including freshwater, brackish and salt marshes. Kinds of marshes were distinguished based on elevation, vegetation and soil and surface moisture. Lists of species characteristic of each type of marsh were provided, but many of the species used to characterize the vegetation of a given kind of marsh were also listed as characteristic of one or both of the other types of marsh. There was no quantification of species abundance or diversity.

Johnston (1955) recognized differing marsh communities along an elevation gradient. He reported that at low elevations a community comprised of *Batis maritima*, *Salicornia virginica* and *Suaeda linearis* graded almost imperceptibly into slightly higher elevations characterized by *Borrichia frutescens*, *B. maritima* and *Monanthochloe littoralis*, which in turn graded into a community of *Spartina spartinae*. Judd et al. (1997a) used multispectral videography to distinguish the pattern of zonation and species composition in a brackish marsh at Laguna Atascosa National Wildlife Refuge (LANWR), Cameron County, Texas. At the lowest elevations there was a distinct zone dominated by maritime saltwort, *B. maritima*. Intermediate elevations supported a zone dominated by shoregrass, *M. littoralis*. At the highest elevations the third zone was dominated by Gulf cordgrass, *S. spartinae*. The upper margin of this zone graded into a shrub-grassland community that occurred on lomas (clay dunes). A salt marsh also was organized into three zones along an elevation gradient and had the same dominant species in each zone (Judd et al. 1997b). Judd & Lonard (2002) compared species richness and diversity in a brackish and salt marsh at LANWR. Forty-seven species were present in the two marshes, but only 15 were common to both. *Monanthochloe littoralis* and *B. maritima* were the dominant species in the brackish marsh and *S. spartinae* was dominant in the salt marsh. In both marshes, four species contributed from 73% to 86% of the cover. Consequently, most species contributed little to vegetation abundance and community structure. There were no significant differences in species diversity within marshes between years or between marshes within a year.

Lonard & Judd (1999) catalogued the vascular plant species found in fresh, brackish and salt marshes in the Rio Grande Delta based on a survey of 27 marshes. They found 84 species representing 27 families were present. Thirty-five species were limited to freshwater marshes and 12 species were limited to salt marshes. No species were unique to brackish marshes. Occurrence in fresh, brackish and salt marshes was provided for each species, but there was no quantification of abundance or comparison of species richness or community similarity among the kinds of marshes.

Marshes of the Rio Grande Delta provide critical habitat for numerous waterfowl species and several threatened and endangered mammalian species. It is important to know the composition, structure, species diversity and fidelity of marsh communities in the Rio Grande Delta to facilitate re-establishment of native vegetation at disturbed sites and to facilitate wise management decisions relative to providing appropriate habitat for marsh fauna. To date, quantified information on species abundance, diversity and community similarity are available for only one brackish and one salt marsh in the Rio Grande Delta. Herein, this study reports on the species composition, species diversity and species richness of 6 freshwater, 9 brackish and 11 salt marshes in the Rio Grande Delta. Community similarity, dominant species, species richness, species diversity and evenness are compared among these marshes.

MATERIALS AND METHODS

The locations of marshes studied are given in Table 1. The line intercept method (Canfield 1941) was used to quantify species abundance. The number of transects sampled at each site was dependent upon the size and configuration of the wetland basin. A minimum of two and a maximum of 10 transects were sampled at the marshes. Transects were established along an elevation gradient extending from the low point in the marsh until an interval with upland vegetation (trees and shrubs) was encountered. Each transect was divided into 10 m intervals and readings were taken along the length of each interval. Each species intercepted by the line was rated individually and was recorded without separation into strata (i.e., tree, shrub and ground layers). Species and foliage cover were recorded and from these data the frequency of occurrence, relative frequency, relative cover and an importance value which is the sum of relative frequency and relative cover were calculated. The importance value was used to determine dominant species.

Table 1. Marshes studied, their locations and mean salinities. NWR = National Wildlife Refuge, TPWD = Texas Parks and Wildlife Department. LANWR = Laguna Atascosa National Wildlife Refuge, NPS = National Park Service.

Marsh	Location	Mean Salinity
Freshwater Marshes		
Paso Real, TPWD	26°18'55.56" N, 97°31'27.48" W	0.5
Russelltown	26°04'51.25" N, 97°34'52.50" W	0.5
Resaca de la Palma, TPWD	25°58'32.86" N, 97°34'00.76" W	0.0
Audubon Sabal Palm Sanctuary	25°51'00.76" N, 97°25'07.15" W	0.0
Cattail Lake, Santa Ana NWR	26°04'32.41" N, 98°09'14.15" W	0.0
Willow Lake, Santa Ana NWR	26°05'00.72" N, 98°08'18.79" W	0.5
Brackish Marshes		
Palo Alto #1, NPS	26°01'17.43" N, 97°28'12.26" W	6.0
Palo Alto #2, NPS	26°00'18.04" N, 97°27'18.55" W	6.0
Laguna Atascosa NWR Resaca	26°10'21.00" N, 97°19'53.55" W	17.0
Olmito Resaca	26°00'48.75" N, 97°32'30.14" W	2.3
Tio Cano #1, NWR	26°12'37.01" N, 97°48'50.43" W	4.5
Tio Cano #2, NWR	26°12'39.36" N, 97°48'47.82" W	3.8
Bayview Resaca #1	26°07'57.80" N, 97°22'56.08" W	6.2
Bayview Resaca #2	26°10'31.67" N, 97°22'59.75" W	9.0
Willamar	26°23'16.56" N, 97°34'59.66" W	dry
Salt Marshes		
Stover Point, LANWR	26°13'01.00" N, 97°19'00.00" W	44.8
Spillway Crossing, LANWR	26°16'00.00" N, 97°23'44.09" W	22.0
Large Marsh, LANWR	26°12'50.79" N, 97°19'52.06" W	20.5
Dry Marsh, LANWR	26°13'00.39" N, 97°19'02.46" W	dry
Osprey Point, LANWR	26°13'58.32" N, 97°21'01.97" W	51.0
Laguna Atascosa Cayo, LANWR	26°14'45.55" N, 97°25'13.12" W	22.0
Redhead Ridge, LANWR	26°10'27.74" N, 97°18'15.67" W	55.6
Rangerville #1, TPWD	26°05'17.22" N, 97°44'25.02" W	25.0
Rangerville #2, TPWD	26°05'08.78" N, 97°44'41.65" W	22.0
Bayview Dry Marsh	26°10'20.32" N, 97°22'55.51" W	33.0
Bayview Brine Marsh	26°10'19.51" N, 97°23'59.73" W	67.5

Similarity of species composition among marshes was calculated using Sørensen's Coefficient of Community (Krebs 1999). Species importance value was used as the measure of abundance for calculating species diversity indices. Species diversity was assessed using the Shannon diversity index (Brower et al. 1998; Krebs 1999). Evenness was determined as the ratio of heterogeneity (H') to maximum heterogeneity (H' max) (Brower et al.; Krebs 1999). One-way analysis of variance was used to compare species richness, species diversity and evenness among the three kinds of marshes (Sokal & Rohlf 1981). Nomenclature follows Jones et al. (1997). Common names follow Hatch et al. (1999).

When surface water was present, salinity readings were obtained with a temperature compensated hand-held refractometer (Table 1). Marshes were classified as freshwater (0.0 to 0.5 ppt), brackish water (0.5 to 17.0 ppt) or saltwater (> 17.0 ppt).

RESULTS

Freshwater marshes.—A total of 81 species were present in the six marshes (Table 2). Species richness per marsh ranged from 15 to 31. No species occurred in all of the marshes, but five species, *Cyperus articulatus* (jointed flatsedge), *Urochloa maxima* (Guineagrass), *Paspalum lividum* (longtom), *Polygonum pensilvanicum* (pink smartweed) and *Typha domingensis* (narrow-leaf cattail) were present in five marshes. The introduced grass, *U. maxima*, was found only in the last interval of transects where the marsh graded into an upland shrub-grassland community. Tree seedlings and scattered shrubs including *Acacia farnesiana* (huisache), *Celtis laevigata* (sugar hackberry), *Ipomoea carnea* (shrubby morningglory), *Mimosa asperata* (black mimosa), *Parkinsonia aculeata* (retama), *Salix exigua* (sandbar willow) and *S. nigra* (blackwillow) were present occasionally in the marshes.

There was a low degree of community similarity among the marshes (Table 3). Coefficients of similarity ranged from 0.103 to 0.525. Resaca de la Palma and Cattail Lake at Santa Ana National Wildlife Refuge (SANWR) were the only marshes that had a coefficient of similarity greater than 0.500. The mean of 15 coefficients of similarity was 0.322 (*SD* = 0.116). Clearly, there were marked differences in species composition of freshwater marsh communities.

Each of the freshwater marshes had a different dominant species (Table 4) and only a few species were responsible for most of the cover. Indeed, the first six species in importance contributed from 72.6% to 96.4% of the relative cover. As with the flora in general, there was low similarity among the marshes in the species making up the six most important species. If each of the six most important species was different in the six marshes, a total of 36 different species was possible; however, 24 different species or 67% of the maximum diversity were found. Nineteen of the 24 species occurred in two or more marshes and 12 occurred in three or more marshes.

Brackish water marshes.—Eighty-one species were present in nine brackish marshes (Table 5). Species richness per marsh ranged from 7 to 24. No species occurred in all of the marshes, but *Borrichia frutescens* occurred in eight marshes (all but Tio Cano #2). No other species occurred in more than six of the marshes (Table 5). There was a low degree of species similarity among most of the marshes (Table 6). The exception was the two resacas at Palo Alto National Battlefield, which had 66.7% of their species in common. These two sites were separated by less than 0.5 km of coastal prairie. Thus, the similarity of

Table 2. Species present in freshwater marshes in the Rio Grande Delta. 1 = Paso Real, 2 = Russelltown, 3 = Resaca de la Palma, 4 = Audubon Sabal Palm Sanctuary, 5 = Cattail Lake and 6 = Willow Lake.

Species	1	2	3	4	5	6
Acacia farnesiana	X					
Alternanthera paronychioides		X	X			
Amaranthus sp.					X	
Ambrosia psilostachya			X		X	
Ammania coccinea	X					X
Bacopa monnieri	X	X				X
Bothriochloa laguroides			X			
Cardiospermum halicacabum			X	X	X	
Celtis laevigata	X					
Chlorocantha spinosa					X	
Chromolaena odorata		X				
Clematis drummondii		X	X			X
Cocculus diversifolius	X					
Commelina erecta	X					
Croton sp.				X		
Cucumis melo					X	
Cynodon dactylon			X		X	
Cyperaceae: unidentified						X
Cyperus articulatus	X		X	X	X	X
Cyperus digitatus	X					X
Cyperus elegans	X					
Cyperus ochraceus	X		X		X	X
Cyperus odoratus	X	X	X	X		
Cyperus rotundus				X		
Cyperus virens		X				
Cyperus sp. (1)	X		X		X	X
Cyperus sp. (2)			X			
Dichanthium annulatum			X			
Dichanthium aristatum					X	
Dichanthium sp.		X				
Eclipta prostrata		X	X		X	X
Echinochloa colona					X	
Echinochloa muricata			X			
Echinodorus beteroi				X		
Eleocharis austrotexana	X					
Eleocharis interstincta	X					X
Eleocharis parvula					X	X
Eleocharis sp.				X		
Eragrostis reptans				X		
Eriochloa punctata	X	X			X	
Helianthus annuus		X	X		X	
Heteranthera dubia	X			X		
Ipomoea amnicola		X				
Ipomoea carnea			X			
Iva annua			X			
Lemna sp.				X		X
Leptochloa fusca	X	X	X			X
Leptochloa nealleyi	X	X				
Leptochloa panicea						X
Ludwigia octovalvis	X				X	
Ludwigia repens						X
Malachra capitata			X	X	X	X
Malvastrum coromandelianum					X	
Marsilea vestita						X
Mikania scandens	X	X				

Table 2. Continued.

Species	1	2	3	4	5	6
Mimosa asperata			X		X	
Panicum hirsutum		X	X	X		
Parkinsonia aculeata		X				
Paspalum denticulatum	X	X	X		X	X
Phyla nodiflora	X				X	
Physalis sp.			X			
Pluchea purpurascens	X	X				
Poaceae: unidentified	X				X	
Polygonum densiflorum	X					
Polygonum pensylvanicum	X		X	X	X	X
Prosopis reptans			X			
Ricinus communis		X				
Rubus riograndis		X				
Salix exigua		X				
Salix nigra				X		X
Schoenoplectus californicus	X				X	X
Sesbania herbacea			X		X	
Sida sp.					X	
Solanum americanum		X				
Solanum campechiense			X	X	X	
Sorghum halepense			X			
Spermacoce glabra	X					
Symphyotrichum divaricatum					X	
Typha domingensis	X	X	X		X	X
Urochloa maxima	X	X	X		X	X
Vigna luteola					X	

Table 3. Comparison of Sørensen's community similarity coefficients among freshwater marshes in the Rio Grande Delta. 1 = Paso Real, 2 = Russelltown, 3 = Resaca de la Palma, 4 = Audubon Sabal Palm Sanctuary, 5 = Cattail Lake and 6 = Willow Lake.

				Sites		
		1	2	3	4	5
	2	0.370				
	3	0.300	0.370			
Sites	4	0.178	0.103	0.311		
	5	0.361	0.218	0.525	0.217	
	6	0.491	0.298	0.415	0.263	0.407

their vegetation is not surprising. Coefficients of similarity for brackish marshes ranged from 0.098 to 0.667 (Table 6). The mean of 36 coefficients was 0.258 (*SD* = 0.123). Thus, the mean similarity for brackish marshes was even less than for freshwater marshes.

Typha domingensis was the dominant species in three brackish marshes (Table 7) and it was a co-dominant in a fourth. *Batis maritima* was the dominant species in two brackish marshes. The six most important species accounted for most of the cover (Table 7). Indeed, the six most important species accounted for 88.0 to 99.8% of the

Table 4. Comparison of species importance among freshwater marshes of the Rio Grande Delta. Freq. = frequency, Rel. Freq. = relative frequency, Rel. Cov. = relative cover, Imp. Val. = importance value (sum of relative frequency and relative cover).

Marsh	Species	Freq.	Rel. Freq.	% Cover	Rel. Cov.	Imp. Val.
Paso Real	*Cyperus ochraceus*	85	15.2	21.36	25.4	40.6
	Eleocharis austrotexana	65	11.6	17.21	20.5	32.1
	Polygonum densiflorum	60	10.7	14.83	17.7	28.4
	Heteranthia dubia	45	8.0	11.23	13.4	21.4
	Leptochloa fusca	60	10.7	7.05	8.4	19.1
	Schoenoplectus californicus	15	2.7	4.77	5.7	8.4
	24 additional species		Total	83.95		
Russelltown	*Urochloa maxima*	70	9.9	21.99	24.0	33.9
	Cyperus odoratus	60	8.5	20.87	22.8	31.3
	Typha domingensis	80	11.3	12.62	13.8	25.3
	Paspalum denticulatum	50	7.0	7.37	8.0	15.0
	Mikania scandens	60	8.5	3.53	3.9	12.4
	Eriochloa punctata	40	5.6	3.59	3.9	9.5
	18 additional species		Total	91.37		
Resaca de la Palma	*Panicum hirsutum*	84.8	17.9	36.11	37.5	55.4
	Typha domingensis	72.7	15.4	20.87	21.7	37.1
	Cardiospermum halicacabum	45.5	9.6	5.20	5.4	15.0
	Paspalum denticulatum	24.2	5.1	7.38	7.7	12.8
	Sesbania herbacea	27.3	5.8	4.75	4.9	10.7
	Solanum campechiense	24.2	5.1	3.93	4.1	9.2
	24 additional species		Total	96.25		
Sabal Palm Sanctuary	*Malachra capitata*	100.0	22.4	24.02	28.7	51.1
	Panicum hirsutum	72.7	16.3	21.82	26.1	42.4
	Echinodorus beteroi	54.5	12.2	14.18	16.9	29.1
	Eleocharis sp.	36.4	8.2	10.27	12.3	20.5
	Heteranthera dubia	45.5	10.2	4.05	4.8	15.0
	Lemna sp.	27.3	6.1	6.36	7.6	13.7
	9 additional species		Total	83.73		
Cattail Lake	*Typha domingensis*	66.7	8.8	16.48	18.0	26.8
	Malachra capitata	66.7	8.8	12.90	14.1	22.9
	Schoenoplectus californicus	46.7	6.1	13.58	14.9	21.0
	Paspalum denticulatum	66.7	8.8	11.07	12.1	20.9
	Phyla nodiflora	66.7	8.8	8.55	9.4	18.2
	Cucumis melo	66.7	8.8	3.75	4.1	12.9
	25 additional species		Total	91.31		
Willow Lake	*Paspalum denticulatum*	75.0	16.0	55.26	62.5	78.5
	Malachra capitata	56.3	12.0	8.59	9.7	21.7
	Bacopa monnieri	37.5	8.0	7.91	8.4	16.4
	Cyperus ochraceus	43.8	9.3	3.61	4.1	13.4
	Eleocharis parvula	43.8	9.3	0.28	0.3	9.6
	Schoenoplectus californicus	18.8	4.0	4.91	5.5	9.5
	17 additional species		Total	88.48		

Table 5. Species present in brackish marshes in the Rio Grande Delta. 1 = Palo Alto #1, 2 = Palo Alto #2, 3 = LANWR Resaca, 4 = Olmito Resaca, 5 = Tio Cano #1, 6 = Tio Cano #2, 7 = Bayview Resaca #1, 8 = Bayview Resaca #2 and 9 = Willamar.

Species	1	2	3	4	5	6	7	8	9
Ambrosia psilostachya			X				X		
Andropogon glomeratus			X						
Atriplex pentandra				X					X
Bacopa monnieri					X	X			X
Batis maritima			X				X		
Bolboschoenus maritimus				X	X		X	X	X
Borrichia frutescens	X	X	X	X	X		X	X	X
Chamaesyce serpens				X					
Chara sp.	X								
Chlorophyta filaments	X								
Chromolaena odorata							X		
Cissus incisa					X		X		
Citharexylum berlandieri			X						
Conoclinium betonicifolium						X			
Cynodon dactylon				X					X
Cyperus articulatus	X	X							
Cyperus ochraceus						X			X
Cyperus sp.				X					
Dalea scandens			X						
Dichanthium sp.							X		
Distichlis spicata			X	X		X	X	X	
Echinodorus beteroi	X	X							
Eclipta prostrata				X					
Eleocharis austrotexana	X	X							
Eleocharis interstincta						X			
Eleocharis sp.						X	X		
Eriochloa punctata							X		
Eustoma exaltatum									X
Forestiera angustifolia			X						
Funastrum cynanchoides						X			
Gossypianthus lanuginosus									X
Havardia pallens			X						
Heliotropium curassavicum		X		X					X
Heteranthera dubia		X							
Hydrocotyle bonariensis						X			
Ipomoea amnicola						X			
Ipomoea sagittata					X				
Isocoma drummondii			X						
Iva annua					X				
Karwinskia humboldtiana			X	X					
Lemna sp.	X								
Leptochloa fusca				X	X	X			X
Leucophyllum frutescens			X						
Limonium carolinianum			X						
Lycium carolinianum	X	X	X	X	X	X			
Machaeranthera phyllocephala			X						X
Malachra capitata					X				
Marsilea vestita	X	X				X			
Maytenus phyllanthoides			X						
Melothria pendula						X			
Mikania scandens				X		X	X		
Mimosa asperata					X				

Table 5. Continued.

Species	1	2	3	4	5	6	7	8	9
Mimosa strigillosa									X
Monanthochloe littoralis		X	X						
Monocotyledon: unidentified									X
Opuntia engelmannii							X		
Panicum hirsutum					X				
Parkinsonia aculeata				X	X				
Paspalum denticulatum	X	X		X	X	X			X
Phyla nodiflora		X				X			
Pluchea purpurascens				X	X		X		X
Poaceae: unidentified				X					
Prosopis glandulosa				X					
Prosopis reptans	X	X	X				X	X	
Rumex chrysocarpus							X		
Salix nigra				X	X				
Schoenoplectus californicus			X						X
Schoenoplectus pungens					X				X
Sesbania drummondii					X				
Sesbania herbacea						X			X
Sesuvium maritimum				X	X				X
Sesuvium sessile				X					X
Sesuvium verrucosum					X				
Solanum elaeagnifolium	X								
Spartina spartinae	X	X	X					X	
Sporobolus virginicus			X						
Sporobolus wrightii							X		
Suaeda linearis			X	X	X		X		X
Symphyotrichum divaricatum				X	X	X			
Typha domingensis	X				X	X	X	X	
Urochloa maxima				X			X	X	

Table 6. Comparison of Sørensen's community similarity coefficients among brackish marshes in the Rio Grande Delta. 1 = Palo Alto #1, 2 = Palo Alto #2, 3 = LANWR Resaca, 4 = Olmito Resaca, 5 = Tio Cano #1, 6 = Tio Cano #2, 7 = Bayview Resaca #1, 8 = Bayview Resaca #2 and 9 = Willamar.

		Sites							
		1	2	3	4	5	6	7	8
	2	0.667							
	3	0.216	0.268						
	4	0.154	0.216	0.217					
Sites	5	0.211	0.167	0.133	0.468				
	6	0.235	0.250	0.098	0.279	0.333			
	7	0.182	0.129	0.300	0.333	0.293	0.222		
	8	0.273	0.300	0.276	0.258	0.200	0.154	0.480	
	9	0.111	0.176	0.176	0.489	0.450	0.250	0.205	0.143

relative cover except in the Olmito marsh where the top six species contributed only 66.7% of the relative cover.

If each of the six most important species was different in the nine marshes, a total of 54 different species was possible. Thirty-one different species or 57.4% of the maximum diversity were found.

Table 7. Comparison of species importance among brackish marshes of the Rio Grande Delta. Freq. = frequency, Rel. Freq. = relative frequency, Rel. Cov. = relative cover, Imp. Val. = importance value (sum of relative frequency and relative cover).

Marsh	Species	Freq.	Rel. Freq.	% Cover	Rel. Cov.	Imp. Val.
Palo Alto #1	*Typha domingensis*	94.4	18.8	41.14	50.4	69.2
	Borrichia frutescens	100.0	19.8	18.66	22.8	42.6
	Eleocharis austrotexana	77.8	15.3	9.37	11.0	26.3
	Paspalum denticulatum	38.9	7.7	6.06	7.2	14.9
	Lycium carolinianum	55.5	11.1	1.53	1.9	13.0
	Marsilea vestita	44.5	8.6	1.95	2.4	11.0
	8 additional species		Total	82.66		
Palo Alto #2	*Eleocharis austrotexana*	93.3	22.2	44.89	59.7	81.9
	Spartina spartinae	40.0	9.5	13.99	18.8	28.3
	Borrichia frutescens	53.3	12.7	6.05	8.6	21.3
	Marsilea vestita	53.3	12.7	5.11	7.2	19.9
	Echinodorus beteroi	53.3	12.7	2.85	3.5	16.2
	Heteranthera dubia	26.7	6.3	0.49	0.8	7.1
	7 additional species		Total	74.49		
LANWR Resaca	*Batis maritima*	71.4	17.0	24.00	26.5	43.5
	Monanthochloe littoralis	48.6	11.6	26.37	29.2	40.8
	Borrichia frutescens	68.6	16.3	12.28	13.6	29.9
	Spartina spartinae	25.7	6.1	14.98	16.6	22.7
	Sporobolus virginicus	40.0	9.5	3.06	3.4	12.9
	Schoenoplectus californicus	22.9	5.4	3.21	3.6	9.0
	16 additional species		Total	90.39		
Olmito	*Leptochloa fusca*	83.3	13.2	12.90	20.9	34.1
	Sesuvium sessile	66.7	10.5	10.04	16.3	26.8
	Pluchea purpurascens	61.1	9.6	5.06	8.2	17.8
	Paspalum denticulatum	33.3	5.3	4.87	7.8	13.1
	Parkinsonia aculeata	55.6	8.8	2.59	4.2	13.0
	Sesuvium maritimum	22.2	3.5	5.76	9.3	12.8
	18 additional species		Total	61.77		
Tio Cano #1	*Typha domingensis*	97.4	22.8	32.44	32.9	55.7
	Schoenoplectus pungens	39.5	9.3	21.31	21.6	30.9
	Iva annua	36.8	8.6	13.53	13.7	22.3
	Lycium carolinianum	71.1	16.7	2.76	2.8	19.5
	Leptochloa fusca	36.8	8.6	7.85	8.0	16.6
	Borrichia frutescens	26.3	6.2	8.90	9.0	15.2
	17 additional species		Total	98.70		
Tio Cano #2	*Typha domingensis*	91.4	17.4	41.94	35.1	52.5
	Eleocharis interstincta	82.9	15.8	32.22	27.0	42.8
	Distichlis spicata	77.1	14.7	24.08	20.1	34.8
	Lycium carolinianum	82.9	15.8	3.53	3.0	18.8
	Eleocharis sp.	28.6	5.4	6.68	5.6	11.0
	Symphyotrichum divaricatum	34.3	6.5	1.75	1.5	8.0
	13 additional species		Total	119.55		
Bayview Resaca #1	*Batis maritima*	87.5	20.0	21.79	29.0	49.0
	Borrichia frutescens	68.8	15.7	19.35	25.8	41.5
	Suaeda linearis	56.3	12.9	8.10	10.8	23.7
	Eriochloa punctata	12.5	2.9	9.13	12.2	15.1
	Distichlis spicata	31.3	7.1	5.70	7.7	14.8
	Pluchea purpurascens	43.8	10.0	2.48	3.3	13.3
	12 additional species		Total	74.96		

Table 7. Continued

Marsh	Species	Freq.	Rel. Freq.	% Cover	Rel. Cov.	Imp. Val.
Bayview Resaca #2	*Borichia frutescens*	83.3	25.0	37.43	33.3	58.3
	Typha domingensis	66.7	20.0	41.07	36.5	56.5
	Distichlis spicata	67.3	20.0	17.05	15.2	35.2
	Spartina spartinae	33.3	10.0	6.28	5.6	15.6
	Bolboschoenus maritimus	33.3	10.0	3.45	3.1	13.1
	Urochloa maxima	16.7	5.0	6.88	6.1	11.1
	1 additional species		Total	112.48		
Willamar	*Sesuvium maritimum*	60.0	23.1	22.51	44.4	67.5
	Sesbania herbacea	22.0	8.3	8.17	16.1	24.4
	Heliotropium curassavicum	34.1	13.0	4.62	9.1	22.1
	Bacopa monnieri	14.6	5.6	5.17	10.2	15.8
	Borrichia frutescens	17.1	6.5	2.95	5.8	12.3
	Pluchea purpurascens	19.5	7.4	1.21	2.4	9.8
	15 additional species		Total	50.66		

Salt water marshes.— Seventy-three species were present in 11 salt marshes (Table 8). Species richness per marsh ranged from 7 to 26. No species occurred in all the marshes, but *B. frutescens* was present in 10. *Batis maritima* and *Prosopis reptans* occurred in nine marshes and *Sporobolus virginicus* was present in eight. Coefficients of similarity ranged from 0.049 to 0.690 (Table 9). The mean of 55 coefficients was 0.372 (*SD* = .147). One-way analysis of variance of coefficients of similarity among freshwater, brackish and salt marshes showed significant variation among the kinds of marshes (i.e., among groups), $F = 7.994$, 2 & 103 *df*, $P < 0.001$. Pairwise comparisons revealed only one significant difference; the mean coefficient of similarity for salt marshes was significantly greater than that for brackish marshes, $t = 3.851$, 89 *df*, $P < 0.001$.

The first six species in importance (Table 10) contributed from 82.2 to 99.4% of the relative cover. *Borrichia frutescens* and *Paspalum vaginatum* each was a dominant species in three marshes and *S. spartinae* and *S. virginicus* each was the dominant species in two marshes (Table 10).

There was greater similarity in the important species of salt marshes than in freshwater or brackish marshes. A list of the six most important species included only 23 different species or 34.8% of the maximum diversity of 66 different species. Freshwater and salt marshes had no dominant species in common (Tables 4 and 10), but brackish and salt marshes shared two dominant species, *B. frutescens* and *Sesuvium maritimum* (Tables 7 and 10). Freshwater and brackish marshes shared one dominant species, *T. domingensis* (Tables 4 and 7).

Table 8. Species present in salt marshes in the Rio Grande Delta. 1 = Stover Point, 2 = Spillway Crossing, 3 = Large Marsh, 4 = Dry Marsh, 5 = Osprey Point, 6 = Laguna Atascosa Cayo, 7 = Redhead Ridge, 8 = Rangerville #1, 9 = Rangerville #2, 10 = Bayview Dry Marsh, 11 = Bayview Brine Marsh.

Species	1	2	3	4	5	6	7	8	9	10	11
Abutilon sp.						X					
Allowissadula lozanii	X					X					
Ambrosia psilostachya	X			X		X	X	X	X		
Atriplex pentandra									X		
Bacopa monnieri									X		
Batis maritima	X	X	X	X	X	X	X			X	X
Bolboschoenus maritimus		X	X			X		X	X		
Borrichia frutescens	X	X	X	X	X	X	X		X	X	X
Bothriochloa laguroides	X	X		X		X	X				
Chara sp.					X		X		X	X	
Chromolaena odorata	X	X	X	X			X				
Clappia suaedifolia							X				
Cressa nudicaulis	X			X							
Croton sp.		X									
Cynanchum barbigerum			X				X				
Cynodon dactylon									X		
Cyperus articulatus	X	X	X								
Desmanthus virgatus	X										
Dichanthium annulatum		X									
Dichanthium aristatum	X										
Dichanthium sericeum		X									
Distichlis spicata		X				X				X	X
Echinocereus sp.	X										
Eriochloa punctata									X		
Gaillardia pulchella	X										
Heliotropium angiospermum	X										
Heliotropium curassavicum									X		
Ibervillea lindheimeri		X									
Isocoma drummondii	X	X				X	X				
Jatropha dioica							X				
Leptochloa uninerva									X		
Limonium carolinianum	X			X	X						
Lycium carolinianum	X	X	X	X	X				X		
Machaeranthera phyllocephala	X		X	X		X			X		
Malvastrum americanum		X									
Malvastrum coromandelianum									X		
Maytenus phyllanthoides	X	X	X	X	X	X	X				
Monanthochloe littoralis	X	X	X	X	X		X			X	
Opuntia engelmannii	X										
Opuntia leptocaulis						X					
Panicum hallii						X					
Paspalum vaginatum		X				X		X			
Passiflora foetida				X							
Pennisetum ciliare					X					X	
Phyla nodiflora	X										
Portulaca pilosa	X										
Pluchea purpurascens		X				X		X	X	X	X
Prosopis glandulosa				X							
Prosopis reptans	X	X	X	X	X	X	X			X	X
Rhynchosia americana	X										
Rhynchosia senna	X										
Ruppia maritima									X	X	X
Salicornia virginica	X	X		X							
Sesuvium maritimum		X				X		X	X		
Sesuvium portulacastrum		X	X				X				

Table 8. Continued.

Species	1	2	3	4	5	6	7	8	9	10	11
Sesuvium sessile			X								
Sesuvium verrucosum			X					X	X	X	
Setaria leucopila						X	X				
Setaria parviflora				X							
Sida sp.								X			
Solanum americanum	X										
Solanum eleagnifolium				X							
Solanum triquetrum				X		X					
Spartina spartinae	X	X	X	X	X					X	
Sporobolus pyramidatus	X										
Sporobolus virginicus	X	X	X	X		X	X	X		X	
Sporobolus wrightii	X	X			X	X	X			X	X
Suaeda linearis	X			X	X	X			X	X	
Trixis inula						X					
Typha domingensis		X			X	X		X	X	X	
Urochloa maxima			X					X		X	
Xylothamia palmeri							X				
Yucca treculeana				X							

Table 9. Comparison of Sørensen's community similarity coefficients among salt marshes in the Rio Grande Delta. 1 = Stover Point, 2 = Spillway Crossing, 3 = Large Marsh, 4 = Dry Marsh, 5 = Osprey Point, 6 = Laguna Atascosa Cayo, 7 = Redhead Ridge, 8 = Rangerville #1, 9 = Rangerville #2, 10 = Bayview Dry Marsh, 11 = Bayview Brine Marsh.

		Site									
		1	2	3	4	5	6	7	8	9	10
	2	0.483									
	3	0.458	0.571								
	4	0.593	0.458	0.526							
	5	0.478	0.500	0.533	0.556						
Site	6	0.429	0.520	0.300	0.435	0.421					
	7	0.440	0.500	0.529	0.450	0.500	0.476				
	8	0.049	0.286	0.160	0.065	0.087	0.364	0.074			
	9	0.231	0.304	0.278	0.286	0.353	0.409	0.211	0.414		
	10	0.298	0.439	0.387	0.324	0.690	0.410	0.364	0.333	0.400	
	11	0.205	0.364	0.261	0.207	0.381	0.387	0.320	0.125	0.222	0.636

Comparison of species richness, species diversity and evenness among marshes.—Values for species richness, species diversity, and evenness are provided for each freshwater, brackish and salt marsh in Table 11. One-way *ANOVA*s for each of these parameters showed no significant differences among the kinds of marshes (Table 12). Freshwater and brackish marshes shared 35 species (coefficient of similarity = 0.216). Brackish and salt marshes had 30 species in common (coefficient of similarity = 0.195), while freshwater and salt marshes shared only 19 species (coefficient of similarity = 0.123). Freshwater and salt marshes had only two important species in common, *U. maxima* and *T. domingensis*.

Table 10. Comparison of species importance among salt marshes of the Rio Grande Delta. Freq. = frequency, Rel. Freq. = relative frequency, Rel. Cov. = relative cover, Imp. Val. = importance value (sum of relative frequency and relative cover).

Marsh	Species	Freq.	Rel. Freq.	% Cover	Rel. Cov.	Imp. Val.
Stover Point	*Spartina spartinae*	31.1	6.8	23.28	36.7	43.5
	Borrichia frutescens	60.6	13.3	5.46	8.6	21.9
	Monanthochloe littoralis	36.1	7.9	8.51	13.4	21.3
	Sporobolus virginicus	27.9	6.1	9.26	14.6	20.7
	Prosopis reptans	45.9	10.0	0.94	1.5	11.5
	Bothriochloa laguroides	14.7	3.2	4.70	7.4	10.6
	26 additional species		Total	63.38		
Spillway Crossing	*Paspalum vaginatum*	65.8	18.7	25.42	29.8	48.5
	Borrichia frutescens	44.7	12.7	12.30	14.4	27.1
	Sporobolus virginicus	28.9	8.2	14.46	17.0	25.2
	Batis maritima	42.1	11.9	8.78	10.3	22.2
	Distichlis spicata	34.2	9.7	8.79	10.3	20.0
	Bolboschoenus maritimus	28.9	8.2	3.50	4.1	12.3
	20 additional species		Total	85.28		
Large Marsh	*Sporobolus virginicus*	55.7	13.9	36.15	36.1	50.0
	Batis maritima	85.2	21.3	19.98	20.0	41.3
	Monanthochloe littoralis	78.7	19.7	20.46	20.4	40.1
	Borrichia frutescens	75.4	18.9	18.66	18.6	37.5
	Lycium carolinianum	50.8	12.7	0.52	0.5	13.2
	Sesuvium portulacastrum	18.0	4.5	0.51	0.5	5.0
	10 additional species		Total	100.06		
Dry Salt Marsh	*Spartina spartinae*	84.4	19.3	76.52	76.3	95.6
	Borrichia frutescens	87.5	20.0	10.24	10.2	30.2
	Prosopis reptans	84.4	19.3	1.47	1.5	20.8
	Monanthochloe littoralis	31.3	7.1	4.22	4.2	11.3
	Salicornia virginica	21.9	5.0	1.70	1.7	6.7
	Cressa nudicaulis	18.8	4.3	0.66	0.7	5.0
	16 additional species		Total	100.27		
Osprey Point	*Borrichia frutescens*	90.0	20.0	33.64	41.1	61.1
	Sporobolus virginicus	70.0	15.6	21.46	26.2	41.8
	Monanthochloe littoralis	50.0	11.1	6.88	8.4	19.5
	Typha domingensis	50.0	11.1	5.70	7.0	18.1
	Batis maritima	60.0	13.3	2.14	2.6	15.9
	Chara sp.	30.0	6.7	1.82	2.2	8.9
	8 additional species		Total	81.81		
Laguna Atascosa Cayo	*Paspalum vaginatum*	65.4	14.8	31.5	31.7	46.5
	Borrichia frutescens	57.7	13.0	16.38	16.5	29.5
	Bolboschoenus maritimus	61.5	13.9	15.02	15.1	29.0
	Distichlis spicata	57.7	13.0	13.47	13.6	26.6
	Suaeda linearis	23.1	5.2	7.95	8.0	13.2
	Sporobolus wrightii	15.4	3.5	4.26	4.3	7.8
	18 additional species		Total	99.25		
Redhead Ridge	*Sporobolus virginicus*	75.0	16.2	35.18	39.2	55.4
	Sporobolus wrightii	54.2	11.7	20.68	23.1	34.8
	Borrichia frutescens	75.0	16.2	14.15	15.8	32.0
	Chara sp.	29.2	6.3	7.87	8.8	15.1
	Batis maritima	45.8	9.9	4.50	5.0	14.9
	Prosopis reptans	45.8	9.9	1.77	2.0	11.9
	12 additional species		Total	89.72		

Table 10. Continued.

Marsh	Species	Freq.	Rel. Freq.	% Cover	Rel. Cov.	Imp. Val.
Rangerville #1	*Paspalum vaginatum*	69.0	37.7	29.63	53.1	90.8
	Sesuvium maritimum	51.7	28.3	16.14	28.9	57.2
	Sesuvium verrucosum	17.2	9.4	4.63	8.3	17.7
	Pluchea purpurascens	13.8	7.5	2.82	5.1	12.6
	Typha domingensis	13.8	7.5	0.87	1.6	9.1
	Urochloa maxima	6.9	3.8	1.36	2.4	6.2
	3 additional species		Total	55.80		
Rangerville #2	*Sesuvium maritimum*	66.7	18.5	20.05	31.9	50.4
	Sesuvium verrucosum	50.0	13.9	8.75	13.9	27.8
	Borrichia frutescens	23.3	6.5	10.78	17.2	23.7
	Sporobolus virginicus	30.0	8.3	6.97	11.1	19.4
	Suaeda linearis	30.0	8.3	4.03	6.4	14.7
	Typha domingensis	23.3	6.5	4.50	7.2	13.7
	14 additional species		Total	62.80		
Bayview Brine Marsh	*Borrichia frutescens*	87.5	24.1	32.51	32.2	56.3
	Distichlis spicata	62.5	17.2	27.46	27.2	44.4
	Ruppia maritima	50.0	13.8	25.11	24.9	38.7
	Batis maritima	87.5	24.1	6.40	6.3	30.4
	Sporobolus wrightii	37.5	10.3	8.41	8.3	18.6
	Prosopis reptans	25.0	6.9	0.26	0.3	7.2
	1 additional species		Total	100.98		
Bayview Dry Marsh	*Borrichia frutescens*	76.9	18.9	20.8	21.2	40.1
	Distichlis spicata	69.2	17.0	19.36	19.7	36.7
	Batis maritima	53.8	13.2	15.53	15.8	29.0
	Chara sp.	30.8	7.5	14.42	14.7	22.2
	Sporobolus wrightii	38.5	9.4	9.85	10.0	19.4
	Typha domingensis	23.1	5.7	7.20	7.3	13.0
	9 additional species		Total	98.26		

DISCUSSION

Only Judd & Lonard (2002) have provided information on species diversity and evenness of Rio Grande Delta marshes and this is for only one salt marsh and one brackish marsh. The marshes they studied are included in the data set of this investigation. Information on species richness is meager. White & Schmedes (1986) identified species "typical" of each of the three marsh types rather than providing a list of all species occurring in each kind of marsh. Thus, they do not provide a measure of species richness. However, if one compares their list of "typical" species with our group of important species (the number of different species in the list of the six most important species), the numbers are similar. For example, White & Schmedes (1986) identified 18 species typical of salt marshes and this study found 23 important species. They report 26 typical species in brackish marshes and this

Table 11. Comparison of species richness (N), species diversity (H′), and Evenness (J′) among freshwater, brackish and salt marshes of the Rio Grande Delta.

Marsh	N	H′	J′
Freshwater Marshes			
Paso Real	30	1.477	0.755
Russelltown	24	1.380	0.857
Resaca de la Palma	30	1.477	0.753
Audubon Sabal Palm Sanctuary	15	1.176	0.788
Cattail Lake	31	1.491	0.839
Willow Lake	22	1.362	0.735
Brackish Marshes			
Palo Alto #1	14	1.461	0.729
Palo Alto #2	13	1.114	0.749
LANWR Resaca	22	1.342	0.760
Olmito Resaca	24	1.380	0.870
Tio Cano #1	23	1.362	0.753
Tio Cano #2	19	1.279	0.735
Bayview Resaca #1	18	1.255	0.803
Bayview Resaca #2	7	0.845	0.880
Willamar	21	1.322	0.766
Salt Marshes			
Stover Point	32	1.505	0.779
Spillway Crossing	26	1.415	0.741
Large Salt Marsh	16	1.204	0.674
Dry Salt Marsh	22	1.342	0.621
Osprey Point	14	1.146	0.801
Laguna Atascosa Cayo	24	1.380	0.774
Redhead Ridge	18	1.255	0.763
Rangerville #1	9	0.954	0.681
Rangerville #2	20	1.301	0.798
Bayview Brine Marsh	7	0.845	0.884
Bayview Dry Marsh	15	1.176	0.837

Table 12. Analysis of variance for species richness, species diversity, and evenness among freshwater, brackish and salt marshes of the Rio Grande Delta.

Parameter & Source of Variation	DF	SS	MS	F (Probability)
Species Richness (N)				
Among Marshes	2	236.425	118.213	2.749 (P > 0.05)
Within Marshes	23	988.960	43.000	
Total	25	1,225.385		
Species Diversity (H′)				
Among Marshes	2	0.110	0.055	1.719 (P > 0.1)
Within Marshes	23	0.727	0.032	
Total	25	0.837		
Evenness (J′)				
Among Marshes	2	0.004	0.002	0.500 (P > 0.5)
Within Marshes	23	0.096	0.004	
Total	25	0.100		

study found 31 important species. White & Schmedes identify 26 species typical of freshwater marshes and this study found 24 are important.

Clover (1937) identified 44 species associated with freshwater habitats in the Lower Rio Grande Valley of Texas, but she did not list species associated with brackish or salt marshes. The number of species she lists for freshwater habitats is far greater than the number of typical species for freshwater marshes reported by White & Schmedes (1986), but far less than the 81 species this study found in freshwater marshes. Only 14 of the 44 freshwater species Clover (1937) identified were found in this study. Conversely, this study found 13 of the 26 species White & Schmedes (1986) listed as occurring in freshwater marshes in freshwater marshes and three others in brackish marshes and this study found 17 of the 26 species they listed for brackish marshes in brackish marshes and four others in salt marshes. This study found 13 of the 18 species they listed for salt marshes in salt marshes. Perhaps this study found a lower percentage of the freshwater species identified by Clover (1937) because there has been a longer time for changes in the flora since her study than there has been since White & Schmedes' (1986) study.

Species composition among marshes of a given type such as freshwater marshes is highly variable even within a relatively small area such as the Rio Grande Delta. Jacobson & Jacobson (1989) found a similar relationship among 18 salt marshes of the Maine coast. Despite the variability in species composition, in most cases one can separate freshwater marshes from salt marshes by the important species present (especially the dominant species). Only two important/dominant species, *T. domingensis* and *U. maxima*, were common to freshwater and salt marshes. *Typha domingensis* clearly exhibits a broad range of salinity tolerance for the species was found in freshwater, brackish and salt marshes. White & Schmedes (1986) list *T. domingensis* as a species characteristic of freshwater marshes and they also found it in brackish marshes, but they do not list it as one of the species occurring in salt marshes in the Rio Grande Delta area. White & Schmedes (1986) do not list *U. maxima* as a species associated with any of the three kinds of marshes. This is likely because the species was uncommon in the Rio Grande Delta area when they did their field investigations, i.e., prior to 1986. Today, *U. maxima* is found on the margins of freshwater, brackish and salt marshes and it invades freshwater and brackish marshes when they begin to dry.

White & Schmedes (1986) noted that brackish marshes are transitional between freshwater and salt marshes and contain some species typical of both marsh types. This current study found that this was certainly so. Of the 32 important species occurring in brackish marshes, 12 also were important in freshwater marshes and 13 were important in salt marshes. *Typha domingensis* and *U. maxima* were important in all three kinds of marshes.

Species richness that was observed in Rio Grande Delta marshes appears to be similar to species diversity in marshes distant from the area. For example, Jacobson & Jacobson (1989) reported that species richness of 18 salt marshes along the Maine coast ranged from 11 to 25 ($\bar{x} = 17.22$, $SD = 4.37$). This study found that species richness in 11 Rio Grande Delta salt marshes ranged from 7 to 32 ($\bar{x} = 18.45$, $SD = 7.38$). There was no significant difference in the means ($t = 0.569$, 27 *df*, $P > 0.5$). Testing the generalizability of the marsh species richness, species diversity and evenness values obtained in this study awaits the reporting of additional information from other areas of the Texas coast.

ACKNOWLEDGMENTS

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PHYSIOLOGICAL TOLERANCE RANGES OF LARVAL *CAENIS LATIPENNIS* (EPHEMEROPTERA: CAENIDAE) IN RESPONSE TO FLUCTUATIONS IN DISSOLVED OXYGEN CONCENTRATION, pH AND TEMPERATURE

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Abstract.—Laboratory experiments were conducted to investigate the physiological tolerance ranges of the mayfly *Caenis latipennis* (Ephemeroptera: Caenidae) from Tanyard Branch Creek in Walker County, Texas in response to stepwise fluctuations in dissolved oxygen concentrations, temperature and pH. Survivorship decreased slightly at a dissolved oxygen concentration of 7.0 mg/L, while trial groups suffered a dramatic decrease in survivorship at a dissolved oxygen concentration of 4.5 mg/L. Mean CTMax (Critical Thermal Maximum) for 10 individuals was 37.8°C with a range from 36.7°C to 38.5°C. Mean critical lower pH for three trials of 10 individuals was 2.56 and mean critical upper pH for three trials of 10 individuals was 12.5.

Assessments of benthic macroinvertebrate communities provide general information regarding the water quality of the streams that support them once baseline information regarding specific streams has been gathered (Edmunds et al. 1976; Hilsenhoff 1977; Barbour et al. 1999; Rabeni et al. 1999; Lydy et al. 2000). However, the ultimate goal of managing stream quality through the practice of bioassessment is the ability to make stream management decisions based on reference data (chemical, physical and biological). These data are typically gathered from a specific region to bypass the expense and time of developing baseline information from each regional stream (Barbour et al. 1999). The cost effectiveness of stream bioassessment versus physical/chemical monitoring is realized only after this baseline information is gathered (Barbour et al. 1999).

A critical requirement of a regionally specific bioassessment program is an understanding of the physiological tolerance ranges of the species comprising the resident benthic macroinvertebrate community. While information exists regarding species specific tolerance ranges, this information is typically anecdotal and not empirically derived (Hilsenhoff 1977; 1982). In addition, many species have large geographical ranges raising the possibility that a continuum of intraspecific physiological tolerance ranges occur. This stresses the necessity for determining regionally specific species tolerance ranges.

Caenis latipennis occurs throughout North America north of Mexico, including south central Canada to extreme southern Texas with a disjunct population in southern Mexico (Provonsha 1990). In a previous study, streams from two neighboring counties in southeast Texas (Walker and San Jacinto counties) were monitored monthly for a period of one year regarding their ephemeropteran community diversity responses to fluctuating physical/chemical parameters. Regression analysis of mayfly diversity against fluctuation of stream quality values indicated that of the eight parameters sampled throughout the period, dissolved oxygen, temperature and pH show the greatest correlation with fluctuating mayfly diversity (Puckett 2003).

The goal of this study was to determine the range of dissolved oxygen, temperature and pH that *C. latipennis* can tolerate with the hope that this information can be used in stream bioassessment practices specific to Walker County streams. The techniques used here may provide a model for further investigations into species specific tolerance ranges. Although this is not an investigation into the potential intraspecific geographical physiological tolerance gradient mentioned above, the data presented here could serve for comparison to similar values obtained for *C. latipennis* in other areas of its distribution.

MATERIALS AND METHODS

Caenis latipennis larvae were collected from Tanyard Branch Creek, taken to the laboratory at Sam Houston State University and allowed to acclimate to laboratory conditions over a period of approximately one week. Mayflies were collected using a standard 0.8 m by 0.8 m kick screen and were transferred to the laboratory in 4 dram vials containing stream water. Larvae were housed in mesh bottomed containers that were submerged in water from the stream in which they were collected. Of the thirty individuals housed in each container, twenty were selected (10 per trial and 10 per control) for both dissolved oxygen and pH experiments. Individuals were selected from the remaining laboratory population for critical thermal maximum (CTMax) experiments.

Dissolved Oxygen Tolerance.—A 2 liter beaker was capped with a 1.5 cm styrofoam disk that was cut to precisely fit the beaker mouth. Holes were then cut in the disk to accommodate the container that housed the mayflies, the connector hose from a N_2 cylinder and dissolved oxygen meter (YSI® Dissolved Oxygen Meter-Model 55/12FT).

The containers that housed the mayflies during the trials were made by first removing the bottoms of two 100 mL plastic cups. A 7.6 cm by 7.6 cm piece of fine mesh was then stretched around the bottom opening of one cup and forced into the second cup. Once taut, this mesh provided an artificial substrate and allowed for a homogenous mixing of water inside and outside of the container. The conical shape of the cups also allowed for a tight fit into the hole in the styrofoam disk which diminished the amount of diffusion of atmospheric oxygen. A plunger to seal off the original opening of this container was built by attaching a 12 cm section of Pyrex® glass cylinder to the center of the removed cup bottom. During trials this plunger was placed into the cup so that it fit snugly beneath the water line, again with the goal of reducing atmospheric oxygen diffusion into the trial beaker. The entire apparatus was placed on a Corning® stirrer/hot-plate. During trials the stir bar revolved at approximately 68 rpm. Stirring the water during trials was essential for the operation of the dissolved oxygen meter.

De-ionized water was used in all trials. Mayflies were placed in DI water three hours before the start of each trial. During the trials dissolved oxygen was removed by purging the water slowly with gaseous nitrogen to lower oxygen levels by 0.5 mg/L increments. Each O_2 level was held for 45 min. until lethal O_2 levels were met. The time interval of 45 min. was determined after subjecting a pre-trial group of ten individuals directly to a dissolved oxygen concentration of 0.5 mg/L. After 40 min. all individuals were dead. Control groups were setup in an identical fashion excluding only the N_2 purge. Ten individuals each in trial and control groups were monitored. All other water parameters remained constant during trials.

Thermal Tolerance.—Determination of lethal maximum temperature levels was carried out in a similar apparatus as that described for dissolved oxygen trials. However, in the temperature trials an aquarium heater and oxygen pump/bubbler were added to the apparatus and the nitrogen component removed. Additionally, the plunger described in the dissolved oxygen trials was removed. Critical thermal maximum (CTMax) trials rely on the observation of a trial endpoint that is specific to the organism being studied (Lutterschmidt & Hutchison 1997). For

Caenis latipennis, observation of lack of righting response followed by the mayfly's inability to cling to the artificial substrate was always followed immediately by death. Inability to cling to the artificial substrate was used as an endpoint in these trials.

Temperature was raised 1.5°C/min. until the endpoint was observed. A total of ten individuals were subjected to these trials. Each trial was performed on one individual per trial while controls were simultaneously run and held at room temperature. As in dissolved oxygen trials, de-ionized water was used. Trial and control individuals were allowed the same acclimation period of approximately 3 hours. All other water parameters remained constant during trials.

pH Tolerance.—pH trials were also carried out in closed beakers. However, in these trials 1 liter beakers were used to minimize chemicals necessary to accomplish stepwise manipulation of pH. Mayflies were housed as described above.

Three trials were run in which a group of 10 individuals were subjected to stepwise fluctuations of pH (both up and down) starting at a pH value of 8.0. Separate trial groups were used for each trial. pH levels were manipulated by titration with 2$\underline{\text{N}}$HCl (pH decrease) and 2$\underline{\text{N}}$NaOH (pH increase). Levels were raised or lowered by half a pH unit per hour. The time period of one hour was decided upon after subjecting a pre-trial group of 10 individuals to water with a pH value of 2. In just under an hour all individuals were dead. VWR Scientific Products® benchtop pH meters (Model SB21) were used to monitor pH levels during trials. Stream water was used in these trials rather than de-ionized water as a result of discrepancy between the pH levels of stream and de-ionized water. Death was signaled by individuals bending at the first abdominal segment accompanied by an inability to remain attached to the artificial substrate. Control groups of ten individuals were run simultaneously. All other water parameters remained constant during trials.

RESULTS

Dissolved Oxygen Tolerance.—When exposed to stepwise reduction of dissolved oxygen, survivorship of *Caenis latipennis* showed a subtle decrease once a dissolved oxygen concentration of 7.0 mg/L was reached. However, a dramatic decrease in survivorship was observed after dissolved oxygen concentration levels were reduced to 4.5 mg/L (Fig. 1a). Mortality continued to increase with relative dissolved

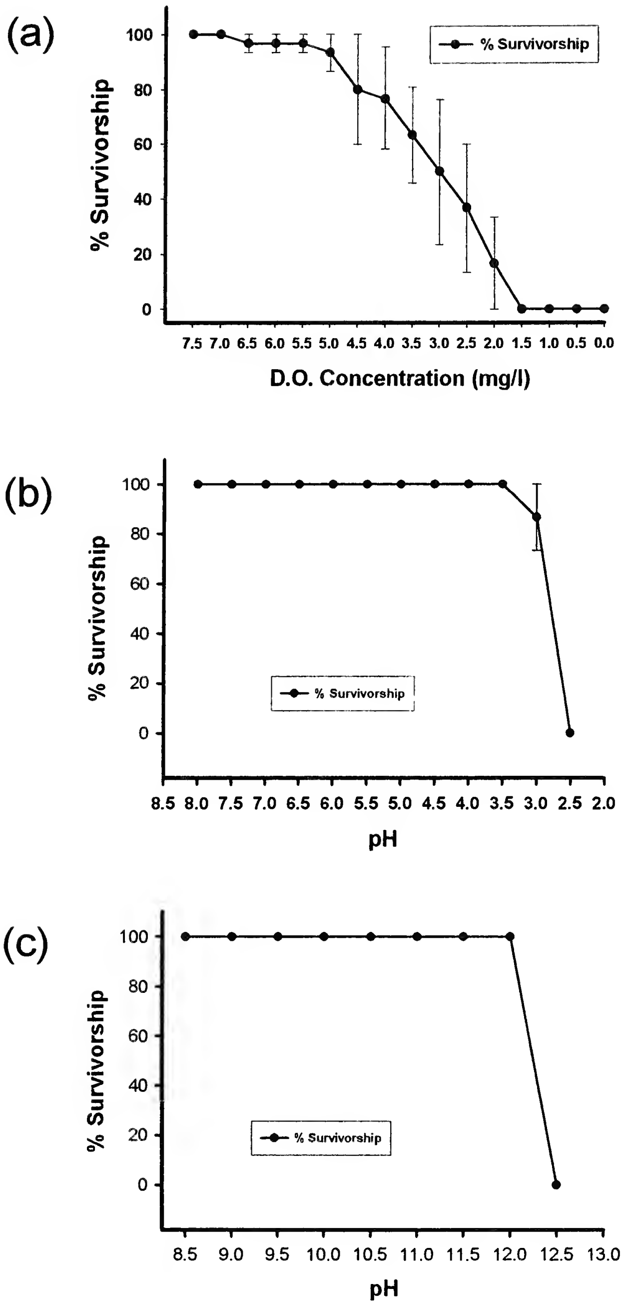

Figure 1. Survivorship of three *Caenis latipennis* (a) dissolved oxygen tolerance threshold trials, (b) pH decrease trials (One-way *ANOVA* on ranks [P=0.795]) and (c) pH increase trials (One-way *ANOVA* on ranks [P=1.000]).

oxygen reduction with no individuals surviving below 1.5 mg/L. Percent survivorship of the control groups during trials 1, 2 and 3 were 80%, 90% and 100% respectively.

Thermal Tolerance.—CTMax trials show that the average upper critical temperature for *Caenis latipennis* is 37.8°C. All ten individuals subjected to CTMax trials died between 36.7°C and 38.5°C. The critical thermal maximum temperature of individuals in these trials was well above the maximum temperature value recorded in the stream during the monitoring period (22.3°C). Controls were run simultaneously at a temperature of 24.5°C with no mortality.

pH Trials.—The critical lower pH level under which *Caenis latipennis* could not survive was 2.5 (Fig. 1b). In two of the three trials all individuals were alive after being exposed to stepwise decrease of pH to a level of 3.0 with 100% mortality after exposure to the same water at a pH of 2.5. During the third trial 40% of the individuals died at pH of 3.0 with the remaining individuals dying at a pH of 2.5. The lowest pH value recorded from a stream during the monitoring period was 7.7. Controls groups were run during the trials in a sample of the same water that was used for trial groups. This water maintained a pH of 8.2 from collection through the end of trials. No mortality was recorded in the control groups.

The critical upper pH level above which *Caenis latipennis* could not survive was 12.5 (Fig. 1c). All individuals in each of three trials were alive after being exposed to stepwise increase of pH to a level of 12.0, after which at a pH value of 12.5 all three groups experienced 100% mortality. The highest pH value recorded during the monitoring period was 8.6. Control groups were run during the trials at a pH of 8.2 in which no mortality was recorded.

DISCUSSION

Caenis latipennis can cope with dramatic fluctuations in pH, dissolved oxygen, and temperature. It is very unlikely that under natural conditions *C. latipennis* larvae would be exposed to water quality parameter values that would fall outside of the tolerance values determined in the laboratory. This suggests a species that should be considered extremely tolerant of a wide range of values pertaining to the water quality parameters investigated in this study. This information is in agreement with previously published pollution tolerance values regarding *C. latipennis* by Hilsenhoff (1987).

The unlikelihood that the values of the parameters investigated here should, in natural systems, fall outside of this species range of tolerance suggests that the utility of *C. latipennis* as an indicator of stream quality is limited. However, when found in systems of low mayfly diversity this species and others found to be similarly tolerant could serve as valuable predictors of acute stream perturbation. At best, *C. latipennis* should be assigned little weight when included in stream assessments based on some biological index such as Hilsenhoffs Biotic Index.

The relative ease with which the range of tolerance values regarding the parameters investigated were obtained suggests that empirically derived tolerance ranges for most Ephemeropteran species can be determined. Due to general similarities in morphology, life history, and ecological requirements, it is likely that these laboratory methods could also be used to gather data regarding physiological requirements of other stream macroinvertebrates such as the orders Plecoptera and Trichoptera. With specific data regarding true tolerance ranges of these insects and other stream invertebrates, bioassessment practices can be approached and interpreted with greater accuracy and relied upon with greater confidence.

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NATURAL HISTORY OF THE SOUTHERN PLAINS WOODRAT *NEOTOMA MICROPUS* (RODENTIA: MURIDAE) FROM SOUTHERN TEXAS

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Abstract.—One hundred forty-eight middens of the southern plains woodrat (*Neotoma micropus*) were excavated from eight study sites on the Chaparral Wildlife Management Area in southern Texas. Several parameters were examined within and between study sites, including sex and age of individuals, demographics of occupancy, and distance between middens. One hundred seventy-seven individuals were captured, with significantly more adult woodrats represented than any other age category. Ninety males and 87 females were captured indicating an equal sex ratio. Analyses revealed that no difference existed in distances between male middens or in distances between female middens. Together, the data suggest no apparent patterns of social structure in woodrats at this study site.

The southern plains woodrat (*Neotoma micropus*) is distributed from southeastern Colorado and southwestern Kansas through western Texas into northern Mexico (Hall 1981; Wilson & Reeder 1993). In Texas, *N. micropus* occupies the western two-thirds of the state, and generally is associated with brushlands of the semi-arid region between the eastern timberlands and the arid deserts to the west (Davis & Schmidly 1994). Woodrats construct middens (nests) from sticks, cactus, and other debris that are arranged into an above ground pile (Finley 1958; Birney 1973). It is common to find aluminum cans, spent ammunition casings, trash, and livestock dung on or within a midden, giving woodrats the nickname "packrat." Below ground (if soil composition/texture permits excavation), a midden usually contains an elaborate tunnel system. In this tunnel system, woodrats store food and nest material, and avoid predation. In areas where non-friable soils do not permit the excavation of tunnels, woodrats often rely on crevices in rocks, decaying timber and canopies of trees for housing. Virtually all middens, whether in trees or below ground, have the characteristic mound of sticks over the opening.

Several studies have been conducted on the systematics and phylogenetic relationships of woodrats (see Edwards & Bradley 2002). However, only a few studies have examined natural history parameters. These indicate that woodrats are solitary and territorial animals (Braun 1989; Conditt & Ribble 1997; Johnson 1952; Raun 1966) with size of territories or home ranges most likely depending on density of individuals and availability of food. Among the most detailed study, to date, is the study by Conditt & Ribble (1997) conducted on *N. micropus* at a research site in south central Texas.

From March 2001 to January 2003, woodrat middens were excavated and occupants captured as part of an ongoing study examining the ecology of the White Water Arroyo arenavirus. Although woodrats were collected under a destructive sampling design, natural history parameters and other life history traits were recorded during the study. The objective of this study was to compare and contrast these natural history attributes (density, distance between middens, sex ratio, number of young, number of animals per midden, and age class distribution) to that available from other studies of *N. micropus*, especially to those of Conditt & Ribble (1997) and Henke & Smith (2000) whose study sites were located approximately 160 km northeast and 175 km southeast, respectively, of the study site examined during this study.

MATERIALS & METHODS

Study sites for this project were located on the Chaparral Wildlife Management Area (CWMA; 28° 20' N, 99° 25' W) that consists of 6,500 ha in the Rio Grande Plains of southern Texas (Ruthven & Synatzske 2002). The CWMA is located approximately 160 km south of San Antonio, between Catarina and Artesia Wells, Texas on Highway 133. The CWMA occurs within Dimmit and La Salle counties with the county border approximately bisecting the property. Soils typically are classified as Duval Fine Sandy Loam (DYB) and Dilley Fine Sandy Loam (DFC) (Stevens & Arriaga 1985). Average annual precipitation is 55 cm with most precipitation occurring between the months of April and September (Stevens & Arriaga 1985). Vegetation (McLendon 1991; Ruthven & Synatzske 2002) includes woody species such as mesquite (*Prosopis glandulosa*) and granjeno (*Celtis pallida*), herbaceous species such as Lehmann lovegrass (*Eragrostis lehmanniana*), fringed singalgrass (*Brachiaria cilliatissima*), and hairy grama (*Bouteloua hirsuta*) as well as a wide array of cactus species (*Opuntia* sp.). Dominant plant species coupled with climatic factors results in classification as a semi-arid acacia-grassland or mesquite-grassland.

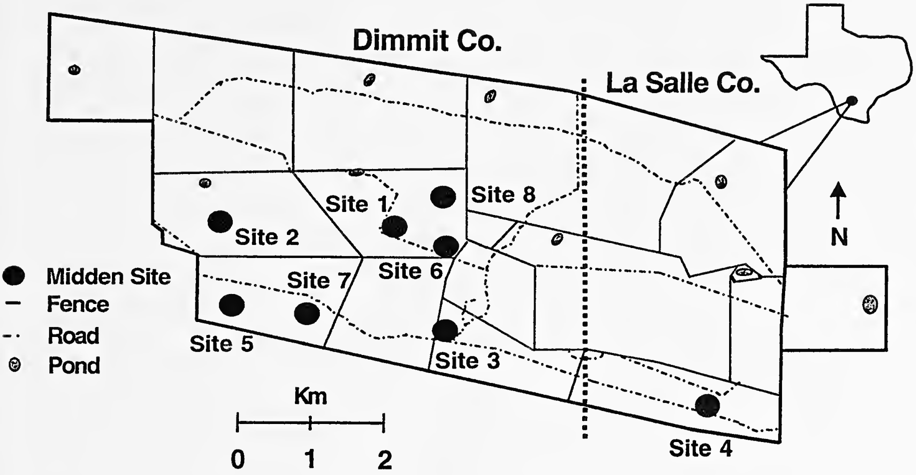

Figure 1. Map depicting the locations of the eight midden sites examined in this study. Dashed line depicts the county line separating Dimmit and La Salle counties and the heavy black line depicts the boundaries of the Chaparral Wildlife Management Area.

The soil composition and availability of food and cover on CWMA provide habitats capable of supporting large populations of woodrats (Finley 1958; Raun 1966). The northern half of CWMA is relatively more open and contains a higher concentration of grassland habitat, whereas the southern half contains a greater concentration of brush. Rotational grazing with cattle occurs yearly during the period October through April. Fire is used throughout the property to control brush and provide livestock and native species with food resources and cover.

Woodrats were captured (by hand) during the excavation of middens located at eight different sites (Fig. 1). Sites were defined as an area possessing suitable habitat for maintaining a high density of woodrats (a high density was required for aspects of the arenavirus study). Sites were selected using a predetermined protocol to provide a relative means of providing a uniform density (high) among sites. Sites for this study (0.2 ha) were circular with a 25 m radius. Sites were not located closer than 500 m from any other site. Once a suitable area was selected, a center point was determined and middens visible along a 25 m transect (in each cardinal direction) were counted. If the number of middens observed along transects was equal to or greater than 10, the site was deemed suitable for excavation. If the number of middens was less than 10, a new site was selected and the protocol repeated. Excavation was

Table 1. Comparison of age and sex across the eight midden sites by collecting date. Roman numbers refer to midden sites. Number of individuals for each age class and sex are in parentheses (males, females).

Site	Date	Number	Age Class			
			Adult	Subadult	Juvenile	Pup
I	Mar 2001	31 (15, 16)	10 (4, 6)	0 (0, 0)	7 (4, 3)	14 (7, 7)
II	Jun 2001	25 (13, 12)	13 (6, 7)	11 (6, 5)	1 (1, 0)	0 (0, 0)
III	Oct 2001	23 (10, 13)	13 (7, 6)	5 (1, 4)	5 (2, 3)	0 (0, 0)
IV	Jan 2002	19 (8, 11)	14 (6, 8)	3 (2, 1)	2 (0, 2)	0 (0, 0)
V	Mar 2002	21 (10, 11)	13 (6, 7)	1 (1, 0)	5 (2, 3)	2 (1, 1)
VI	Jun 2002	20 (10, 10)	13 (6, 7)	3 (2, 1)	4 (2, 2)	0 (0, 0)
VII	Oct 2002	19 (11, 8)	12 (6, 6)	4 (4, 0)	3 (1, 2)	0 (0, 0)
VIII	Jan 2003	19 (13, 6)	16 (10, 6)	2 (2, 0)	1 (1, 0)	0 (0, 0)
Total		177 (90, 87)	104 (51, 53)	29 (18, 11)	28 (13, 15)	16 (8, 8)

conducted four times per year (January, March, June and October) over a two-year period (Table 1). Each site was excavated only once during the study; and all sites were excavated during a single trip to circumvent seasonal biases.

Every midden within the boundaries of each site was excavated, regardless of appearance. Because of the potential for an extensive tunnel system within a midden, every tunnel was excavated to its termination point to ensure that all individuals were captured from the midden or to determine if the midden truly was uninhabited. Universal Transverse Mercator (UTM) coordinates were recorded with a hand-held GPS unit for each midden excavated regardless if midden was inhabited or vacant. These coordinates were later used to map each site to establish a geographical perspective (Fig. 2).

If an individual woodrat escaped during the excavation of a midden, an immediate effort was made to recapture it. Excavation activities were conducted during daylight hours when rodent activity was lowest (woodrats are nocturnal). Each captured woodrat was assigned a TK number (Museum of Texas Tech University identification number), weighed, sexed, aged, reproductive status determined and locality (UTM) recorded. Ages were catagorized as adult, subadult, juvenile, and pup based on molting pattern (adult versus subadult), size/mass (subadult versus juvenile), and attachment to mammae (juvenile versus pup). Animals were either sacrificed (voucher specimens deposited in the Museum at Texas Tech University) or transported to the University of Texas Medical Branch at Galveston, Texas for inclusion in a prospective study on the biology of arenaviruses in *N. micropus*.

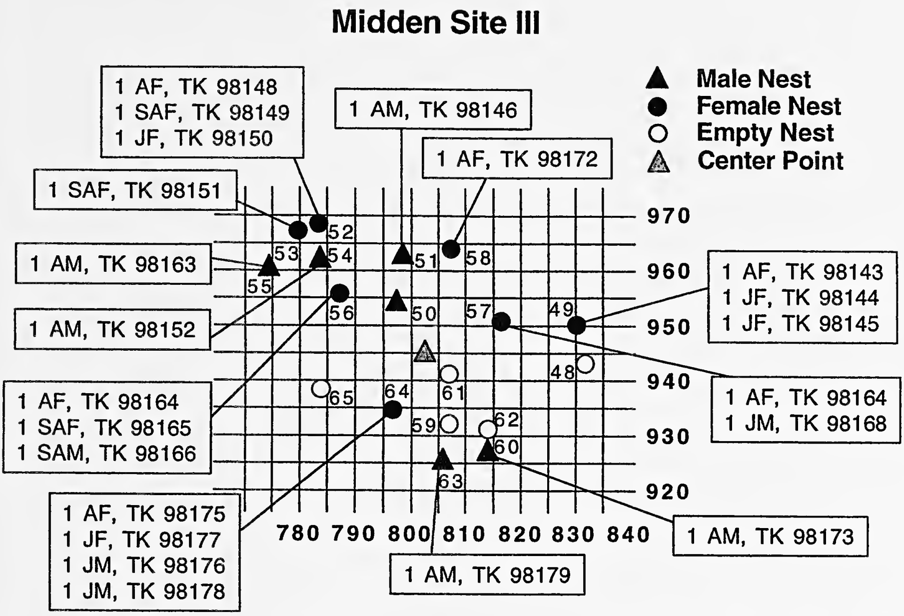

Figure 2. Map of Midden Site III. Distance between grid lines is 5 meters. Spatial relationships between middens were constructed using UTM coordinates collected in the field (maps are oriented using north and east corrdinants). The labels include age class, gender, and museum identification number (TK) of the woodrats collected from the middens. Abbreviations include: AM = adult male, SAM = subadult male, AF = adult female, SAF = subadult female, and J = juvenile.

The Chi-square test (χ^2) and Student's *t*-test were performed, among midden sites and within midden sites, to test for statistically significant differences in age, sex, distance from other middens, etc. For examining differences between the distribution of adult male and female woodrats, a gender-specific centroid was calculated for each midden site using UTM coordinates collected in the field. The distance of each midden from the corresponding centroid was measured in meters, and the mean of the adult male woodrat-centroid distances was compared to the mean of the adult female woodrat-centroid distances using a RankSum test. Middens that were co-occupied by adults of different sexes were not included in this study.

RESULTS

One hundred forty-eight middens were excavated and 177 individuals were captured (Table 1). Five escapees, that were not recaptured,

Table 2. Mean distances between middens occupied by adult male or adult female woodrats, by site. Ranges are in parentheses.

Site	Number of middens	Male Mean distance	Number of middens	Female Mean distance
I	4	19.5 (16.8-24.1)	5	14.2 (9.8-20.5)
II	7	7.9 (1.4-15.5)	7	8.2 (5.0-15.6)
III	6	8.8 (7.2-11.0)	7	11.4 (2.0-23.2)
IV	5	14.0 (10.6-17.2)	9	12.9 (5.0-17.1)
V	7	14.7 (12.5-11.1)	7	9.9 (2.8-16.4)
VI	7	7.3 (5.0-7.2)	6	7.7 (3.0-28.2)
VII	8	5.8 (4.2-7.2)	6	9.3 (3.6-13.6)
VIII	11	7.9 (3.6-13.9)	6	14.8 (11.0-19.7)

occurred during the study. Number of captures by site ranged from 19 to 31 and number of middens per site ranged from 11 to 23.

Age.—Individuals were separated into four age classes (adult, subadult, juvenile and pup) resulting in 104 adults (58.8% of the total population), 29 subadults (16.4%), 28 juveniles (15.8%), and 16 pups (9.0%) being captured. Comparison of age classes (Table 1) revealed a difference in the number of individuals within age classes across sites ($\chi^2 = 90.39$, $df = 21$, $P < 0.001$), with adults typically being more numerous than either subadults, juveniles or pups. However, in Site I, adults and pups were more numerous than subadults or juveniles and in Site II, adults and subadults were more numerous than juveniles or pups.

Sex.—Ninety males (50.8% of the population) and 87 females (49.2%) were captured (Table 1). A *t*-test revealed no difference between the number of males and females across the eight middens ($t = 0.32$, $df = 15$, $P > 0.05$) or in a comparison of sex by age class ($t = 0.35$, $df = 3$, $P > 0.05$). No differences ($\chi^2 = 100.49$, $df = 45$, $P > 0.05$) were found between sexes by age class over the eight midden sites.

Distances between middens.—Calculation of distances between middens (nearest-neighbor distance) were calculated from UTM coordinates as shown in (Fig. 2). Estimates from all study sites (Table 2) resulted in a mean of 6.58 m (range: 1.70 - 14.12 m). Mean distance between male middens for the eight study sites was 10.75 m (range: 7.23 - 16.40 m), whereas mean distance between female middens was 11.05 m (range: 5.16 - 19.49 m). No significant difference in distance was detected between each midden among the eight sites (χ^2, $P > 0.05$ for each of the eight sites), between sexes within sites (*t*-test, $P > 0.05$ for each of the eight sites), or in mean differences between sexes among the

Table 3. Average distances between middens occupied by adult woodrats and gender-specific centroids, by midden site. The number of males or females captured is in parentheses.

	Midden site								
Gender	I	II	III	IV	V	VI	VII	VIII	Overall
Male	16.9 (4)	15.3 (6)	20.7 (7)	18.0 (6)	20.2 (6)	10.9 (6)	16.0 (7)	16.3 (10)	18.5 (52)
Female	15.7 (5)	17.8 (7)	20.3 (6)	22.6 (8)	18.1 (7)	16.6 (7)	14.8 (5)	20.2 (6)	16.8 (51)

eight sites ($t = 0.22$, $df = 7$, $P > 0.05$). Middens containing both adult males and adult females were excluded from this analysis, as it was impossible to determine whether the male or female was the primary occupant of the midden.

The means of midden-centroid distances of male and female woodrats were 18.5 m (range: 3.9 - 32.6 m) and 16.8 m (range: 5.6 - 31.9 m), respectively. The results of a RankSum test (Table 3) indicated that there was no statistically significant difference (Type I error = 0.10) between the mean midden-centroid distance of male woodrats and the mean midden-centroid distance of the female woodrats.

Middens/site.—Average number of middens per site was 18.37. No differences were identified between number of middens per site ($t = 0.00$, $df = 7$, $P > 0.05$), number of male middens versus female middens among sites ($\chi^2 = 3.13$, $df = 7$, $P > 0.05$), or number of male middens versus female middens within sites ($t = 0.27$, $df =$ xx, $P > 0.05$). Site VIII contained the greatest number of middens (23), whereas Site I had the fewest (11). Site I had the largest number of individuals (31) and Sites IV, VII and VIII had the fewest (19).

Occupancy per midden.—One hundred six of the 148 excavated middens (71.6%) were occupied. Calculations of multiple occupancy, (how many individuals of each age class and sex occupy the same midden), indicated that adult females and their young were found together on 27 (18.2%) occasions. Using number of pups as a baseline, the average litter size is two (27 females with 54 pups). Adult females and adult males were found in the same midden 13 (8.7%) times. The greatest number of individuals found in a single midden was six and five middens contained five individuals.

DISCUSSION

Several parameters were examined and only age class structure varied statistically by site, season or between years. The adult age class (n = 104) contained the highest number of individuals and the pup age class contained the least (n = 16). Interestingly, pups were collected only in March indicating a peak reproductive effort in late winter or early spring; however, the presence of juveniles during other months suggests that some reproduction occurs throughout the year. In addition, this time frame corresponded to the population peak in February reported by Conditt & RIbble (1997). However, reproductive efforts appeared to taper off more rapidly in this study than reported in Conditt & Ribble (1997), where the number of lactating or pregnant females peaked at 50% in October.

Because of the idea that the woodrats might have a polygynous or promiscuous mating system (Conditt & Ribble 1997), it was assumed that the number of females collected would be more numerous than males. As indicated, there was no significant difference in the overall number of males (90) compared to females (87) or in any age class. The ratio of adult males to females was 1:0.97; whereas, the study by Conditt & Ribble (1997) reported a ratio of 1:1.16.

The social structure within the midden itself was another aspect of the study that did not hold true with assumptions pertaining to woodrat habits. The most surprising finding was that adult males and adult females being captured within the same midden. Conditt & Ribble (1997) never observed more than one adult woodrat in a midden at the same time. However, during this study, an adult male and an adult female were observed in 13 middens. There are at least two possibilities to explain this. The simplest would be that the male was there solely for mating purposes. Although this may be true, all middens were excavated during daylight hours, and *N. micropus* is a nocturnal species. Because of this, several questions arise as to the social habits of *N. micropus*. How long does courtship take place, perhaps they stay "overday." Second because of high densities of woodrat middens on CWMA, perhaps adult males and females cohabitate. Parameters of this study do not provide significant conclusions to these questions.

Because of the direct capture of all individuals throughout all midden sites, one aspect of their natural history that could not be measured is home range. Studies by Henke & Smith (2000) and Conditt & Ribble (1997) that examined home range within *N. micropus* found the home range of males to be 1696 m^2 and 1829.2 m^2, respectively. Female home range was found to be significantly less at 188 m^2 and 258.2 m^2, respectively. Although one could not calculate home ranges due to the destructive sampling design of this study, the data are not consistent with a harem mating system. Instead, maps of each midden site revealed no visible patterns that would support social structure regarding midden placement or midden selection by males or females. In addition, if a polygynous or promiscuous mating system existed, average distances between male middens and average distances between female middens should differ. For example, there should be a "standard" distance between male middens and to a lesser degree for female midden distances. Statistical tests failed to support this hypothesis.

In addition, the number of woodrats per hectare in this study was 110.6 and the number of middens per hectare was 92.5. The number of adult males was 31.9 and the number of adult females was 33.1 per hectare. These numbers are much greater than that found (2.0 woodrats per hectare in October to 5.5 per hectare in February) by Conditt & Ribble (1997). One possible explanation for the large increase is that this study was biased for high densities of woodrat middens; these numbers obviously would be lower if sites had been selected at random. Due to the large numbers of woodrats per hectare and abundance of resources, home ranges of woodrats on CWMA are most likely not that large. When superimposed (not shown) on a map of the midden sites (produced in this study), the home ranges reported by Conditt & Ribble (1997) and Henke & Smith (2000) for a single individual would extend well beyond the boundaries of the entire midden site. This is somewhat surprising given the similarities in habitats and geographic proximity of the three studies.

This study answered several questions regarding the natural history of *N. micropus*. Because of suitable habitat conditions, CWMA is ideal for sustaining large populations of woodrats. The large amount of food and cover resources available to woodrats on CWMA enable populations to not only survive but do so in such close proximity with each other that early predictions on habits and social structure simply do not apply.

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ADULT FORAGING BEHAVIOR IN MEARNS' GRASSHOPPER MOUSE, *ONYCHOMYS ARENICOLA* (RODENTIA: MURIDAE) IS INFLUENCED BY EARLY OLFACTORY EXPERIENCE

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Abstract.—Studies were conducted to assess the effects of early exposure to food-borne olfactory cues and subsequent searching behavior and odor preferences in adult males of the grasshopper mouse, *Onychomys arenicola.* Twenty-day old mice were randomly assigned to 1 of 3 treatment groups: a control group (CG) was fed on crickets (*Acheta domesticus*) and mealworms (*Tenebrio molitor*). Another group (EG) received an enriched diet of crickets, mealworms, roaches (*Periplaneta americana*), and commercial dog and cat chow. The IG group received an impoverished diet consisting only of crickets. These feeding regimes continued for 80 days. Mice were then presented with odor choice tests in a Y-maze olfactometer. Mice from each treatment group were tested for their choices between known and novel prey odors (NPO), and between known odors and a novel pure chemical odor (NCO). Control mice exhibited a preference of 70% for the known prey odor (cricket) and only 30% for the NPO (wolf spider, *Hogna carolinensis*). In contrast, EG mice showed a significantly higher preference (70%) toward the NPO. Only 20% of the IG animals chose the NPO. In addition, EG mice made decisions on which odor to investigate significantly faster than CG or IG animals. These results indicate that *O. arenicola* relies on olfactory cues when making decisions concerning prey choice during foraging bouts. They also suggest that knowledge of olfactory cues associated with prey is not innate in this species, but is acquired during early sensitive periods of development (olfactory imprinting). This is the first demonstration of olfactory imprinting in a murid rodent within the genus *Onychomys*.

Previous studies have shown that early olfactory experience can affect the subsequent foraging behaviors or prey choice of adult predators including insects (Chapman et al. 1987), spiders (Punzo & Kukoyi 1997), rock crabs (Rebach 1996), turtles (Punzo & Alton 2002), lizards (Punzo 2003a), polecats (Apfelbach 1973), ferrets and other mustelids (Apfelbach 1992), murid rodents (Berdoy & Macdonald 1991), shrews (Churchfield 1990; Punzo 2003b) and canids (Weldon 1990). Furthermore, a study on the ferret *Mustela putorius* showed that olfactory imprinting may be involved because certain odors encountered by young animals during sensitive periods can serve as acquired sign stimuli for subsequent prey identification and selection (Apfelbach 1992). However, little information is available on the effects, if any, of early olfactory experiences on subsequent foraging behavior in murid rodents (Frank & Heske 1992).

Mearns' grasshopper mouse, *Onychomys arenicola* (Rodentia: Muridae) is an inhabitant of low desert areas in west Texas. They prefer foothills, xeric flats and mesquite-covered mesas with sandy soils (Whitaker 1996), and feed primarily on a variety of arthropods and small vertebrates as well as seeds (Horner et al. 1965; Brown & Zeng 1989; Punzo 2000). The purpose of the present study was to assess the influence of early olfactory experience on subsequent searching behavior and odor preferences of adults of *O. arenicola*.

MATERIALS AND METHODS

All animals used in these experiments were the second or third generation offspring of adults originally collected from several localities within a 4 km radius of Redford, Texas (Presidio County) in 1999 and 2000. This area lies within the northern region of the Chihuahuan Desert. The experimental protocol used in this study was similar to that employed by Apfelbach (1978). To summarize, 10 newly weaned mice were randomly assigned to each of three groups, all of which were fed a diet of crickets (*Acheta domesticus*) and mealworms (*Tenebrio molitor*) until they were 20 days old. After this time, each group was fed on a different diet regime until the age of 80 days. A control group (CG) continued to receive crickets and mealworms; another group (EG) was fed an "enriched" diet consisting of crickets, mealworms, roaches (*Periplaneta americana*) and commercial cat and dog chow (Ralston Purina, St. Louis, MO). An impoverished group (IG) received only crickets. In addition, to enhance olfactory deprivation, the IG group was exposed to an artificial olfactory environment saturated with the odor of geraniol. It has been reported that the continuous exposure to a single predominant odor can mask the ability of an animal to experience other environmental odors resulting in what has been termed a state of olfactory deprivation (Weldon 1990).

Behavioral studies were conducted on adult males from the three

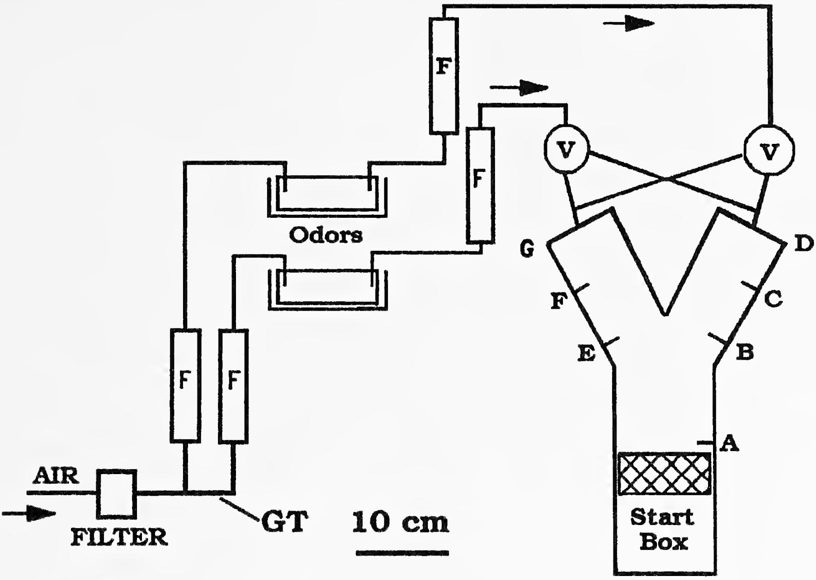

Figure 1. Diagram of the Y-maze olfactometer used in odor choice experiments. GT = glass tubing; F = flowmeters; V = valves. Arrows indicate direction of air flow. See text for details.

groups (*n* = 10/group) when they reached 7 months of age. These animals were tested in a Y-maze olfactometer to determine if there was any preference shown toward certain odor cues. Two tests were given to each animal: one in which the subject was given a choice between a known prey odor and a novel prey odor, and another test where the choice was between a known prey odor and a novel pure chemical odor. There was a 10 min delay between tests. The general procedure was similar to that employed by Apfelbach (1992). To summarize, the olfactometer consisted of a Y-maze constructed of plexiglass (Fig. 1) connected to sources of odor via glass tubing (GT). The air and odor flow were controlled through the use of flowmeters (F) located before and after the odor saturators (odors). Teflon valves (V), located at each end of the Y-maze, were used to control the direction of flow of the odors. Test odors were randomly introduced into the left or right end of the maze before a mouse was allowed to leave the start box. Test odors consisted of a known prey odor (cricket), a novel prey odor (wolf spider, *Hogna carolinensis*) and a novel pure chemical odor (oil of wintergreen). At the start of each trial an individual mouse, food-deprived for 72 hr, was placed into the start box and allowed to remain

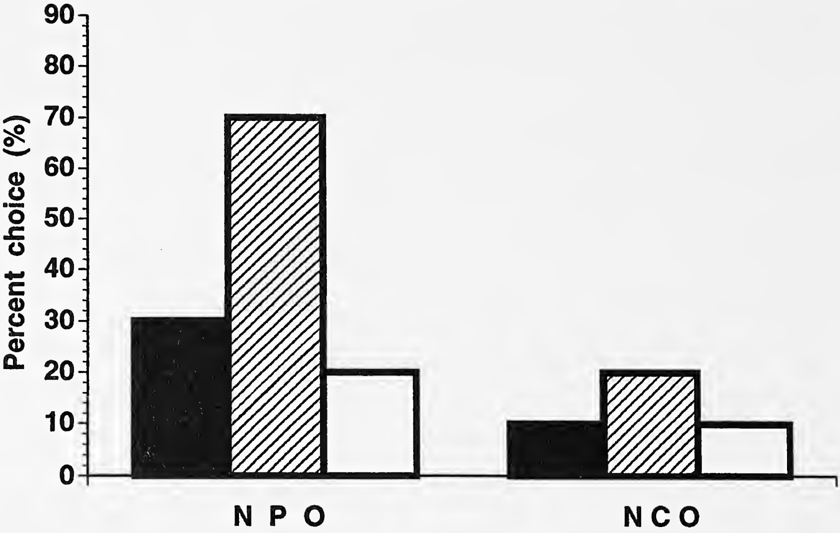

Figure 2. Percent choice (percent of trials in which animals explored the novel odors) of adult males of *Onychomys arenicola* toward novel prey (NPO) and novel chemical (NCO) odors. Data show that EG animals (experienced an enriched diet) exhibited a greater tendency to explore novel odors as compared to the control (CG) and impoverished (IG) groups. Black bars = CG (control) group; stippled bars = enriched group (EG); unshaded bars = impoverished group (IG).

there for a period of 10 min. The start box door was then lifted, and the mouse was allowed to enter the maze. A record was made of which arm of the maze was chosen (% choice) for each trial, as well as the time (sec) needed for a mouse to make its decision. An arm was considered chosen if the animal moved into it at least as far as point C or F. All observations were made behind a one-way mirror to minimize disturbance to the animals.

Data on odor preference tests and time needed to make a decision were analyzed using Chi-Squared and Kruskal-Wallis tests (Sokal & Rohlf 1995).

RESULTS

The results of the odor preference tests are shown in Fig. 2. In the choice condition of known prey odor (crickets) versus novel prey odor (NPO; wolf spiders), control animals (CG) exhibited a preference of 30% toward the NPO, and 70% to the cricket odor. In contrast,

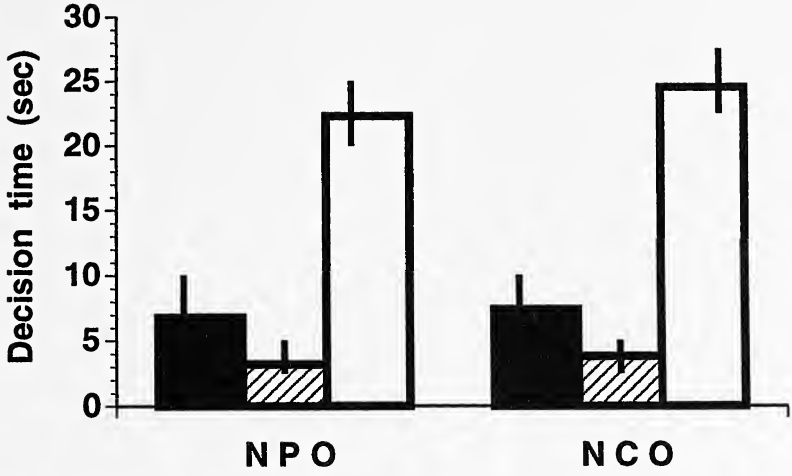

Figure 3. Amount of time (sec) required for males of *Onychomys arenicola* to make a decision as to which odor to choose. Data are expressed as means + *SD* (n = 10/group). Black bars = CG (control group); stippled bars = enriched diet group (EG); unshaded bars = impoverished group (IG); NPO = novel prey odor; NCO = novel pure chemical odor.

animals exposed to an enriched diet (EG) showed a preference of 70% toward the NPO, whereas only 20% of the IG animals chose the NPO. The differences between the CG and EG, and between CG and IG were significant ($P < 0.01$). In addition, novel chemical odors (NCO) were less attractive to these mice than were novel prey odors.

The time needed by these animals to make a decision as to which odor to investigate is shown in Fig. 3. In the choice condition of known prey odor vs. NPO, mice exposed to the enriched diet (EG) made decisions significantly faster than controls ($P < 0.01$) and IG ($P < 0.001$) animals. Similar results were obtained when a novel chemical odor (NCO) was presented rather than a NPO.

DISCUSSION

These results indicate that the cricetid rodent *Onychomys arenicola* utilizes olfactory cues when making decisions during foraging bouts. They also suggest that knowledge of olfactory cues associated with prey is not innate in this species, but is acquired during early periods of development. This type of olfactory imprinting on cues associated with prey or other food items has been reported for animals from a diversity of taxa including insects (Thorpe 1939; Chapman et al. 1987), spiders (Punzo & Kukoyi 1997), turtles (Burghardt & Hess 1966; Punzo & Alton 2002), lizards (Punzo 2003a), polecats (Apfelbach 1973), ferrets (Apfelbach 1992), and murid rodents (Berdoy & Macdonald 1991). To the author's knowledge, this is the first demonstration of olfactory imprinting in a murid rodent within the genus *Onychomys*.

It has been argued that the ability to imprint on specific environmental cues during an early sensitive maturational period would allow an animal to combine the advantages of hardwired specialist feeders with those of generalists who rely to a greater extent on learning (Johnston 1982; Stephens 1991). The situation whereby a predator is exposed to only a small number of prey items during some early sensitive period of life might facilitate the formation of an olfactory search image, thereby focusing food searching behavior for specific prey (Burghardt 1993). Thus, even though an animal may have the capacity to feed on a variety of food types (broad trophic niche), by concentrating on a single, abundant and reliable food encountered early in life, individuals would minimize energy costs associated with trial-and-error learning while benefiting from the increased foraging efficiency associated with having a single search image to facilitate hunting. In these experiments, grasshopper mice that were exposed to only a small number of prey objects early in life, did not respond strongly to novel prey odors and even less to a novel chemical odor, both of which convey less important olfactory information.

Onychomys arenicola is found in xeric habitats, where seasonal fluctuations in prey availability are common (Punzo 2000). Although it is a generalist predator that feeds on a variety of arthropods, small vertebrates and seeds (Horner et al. 1965; Brown & Zeng 1989; Whitaker 1996), the ability to form an early search image associated with one or a few prey types that may be more locally abundant and available, would contribute to its overall fitness.

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ROBOTICS REPEATABILITY AND ACCURACY: ANOTHER APPROACH

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Abstract.—Repeatability is one characteristic of a robot, which is of tremendous importance. In this paper the concept of repeatability is clearly defined in terms of the standard deviation of the random component of the error of a robot in returning to a taught position and accuracy is defined in terms of the mean error as a function of three important variables. Data used to estimate repeatability and accuracy were obtained from a full-factorial experiment in which speed, payload and amount of axis movement were used as independent variables. The robot used to furnish data for this research was a PUMA 560. A regression model was developed to estimate the accuracy at various factor levels and the repeatability was determined to be 0.0036 inches. The statistical analysis clearly indicated that all three factors, as well as their interactions, affect the accuracy of the robot. The regression model indicated that approximately 35% of the radial error variability was explained by the linear model and 65% of the radial error was due to repeatability.

The performance of a robot is highly dependent upon both the repeatability and the accuracy of the robot. Repeatability is the robot's ability to return to a previously taught point (Rehg 1985). Repeatability is especially important in assembly applications of robots and has a critical effect on product quality since product tolerances are decreasing (Khouja & Kumar 1999). Specifications on robots are often obtained from robot vendors, but the problem with the use of these data is that the user does not know the conditions under which they are tenable. It is therefore necessary to investigate the interaction among various robot process variables and determine the conditions under which a given mix of values can be achieved (Offodile & Ugwu 1991).

Repeatability and accuracy are often confused and rarely defined in a clear and unambiguous way. Necessarily, both accuracy and repeatability must be estimated by using the error made by the robot when trying to return to a previously taught point. This error is defined to be the radial distance from the previously taught point to the point at which the end effector comes to rest. The method for estimating accuracy and repeatability in this research will depend upon errors obtained experimentally by varying the speed, the weight of the payload and the amount of axis movement. More specifically, for any combination of the three variables the accuracy will be defined as the mean of the distribution of errors for that combination. As a result of this definition, accuracy is constant for any fixed combination of speed, weight and amount of axis movement. Therefore, accuracy has no connection to the variability of the distribution of errors. The repeatability of a robot does depend on the variability of the distribution of errors. In fact, repeatability will be defined to be equal to three times the standard deviation of the distribution of errors.

The definitions of accuracy and repeatability in the above paragraph indicate that the mean of the distribution of errors depends on the values of the variables while the standard deviation does not. Therefore, the variation in the errors due to changes in the mean as a result of changes in the three input variables must be removed in order to estimate accuracy and repeatability. The standard mechanism for this task is a model for the means developed by using statistical techniques on data obtained from a designed experiment.

MATERIALS AND METHODS

The parameters speed, payload and percentage of axis movements were varied on a PUMA 560 robot using different combinations to estimate accuracy and repeatability. A conventional X-Y-Z Cartesian coordinate measurement system was used. The points of movements to the X, Y and Z gauges were found by driving each of the six axes to different percentages of axis movements. Errors were measured using precision gauges for the X, Y and Z coordinates. A test stand was constructed for this experiment similar to the one discussed by Warnecke & Schraft (1982). The test stand was securely clamped down to a table that was leveled. The test stand allowed measurement of X, Y and Z deviations using three Mitutoyo dial indicator gauges. The three gauges used have flat faced contact plates. The resolution of the Mitutoyo gauges used is 0.0001 inches with a 0.25 inch stroke. The deviations were expected to be in the 0.001-0.004 inches range. The rule of "10" was therefore applied. This means the gages have a resolution 10 times the expected reading. The temperature in the laboratory was kept at a constant 71° F which is very close to the desired 68° F for precision measurements (DeGarmo et al. 1997).

The three parameters weight, speed and percent of movement in each axis were varied at three different levels designated low, medium and high. A total of 27 different combinations were used. The PUMA robot used had six different axes.

Weight.—The payload of the PUMA robot used was 2.5 kg (5.5 lbs). This did not include the gripper. Four "one" lb weights and two "0.5" lb weights were used. A special designed fixture that can be attached to the wrist was used for varying the weight. It included a precision ground 0.5000 inch diameter +/- 0.0001 inch precision tooling ball. The tooling ball probe has a small "negligible" weight. The probe was locked in position so no movement was available in the X, Y and Z direction. The following loads were used in this experiment: low (1.5 lbs ≈ 30% of the payload), medium (3.0 lbs ≈ 60% of the payload) and high (4.5 lbs ≈ 90% of the payload).

Speed.—Maximum speed of this robot was 0.5m/sec, which is equivalent to an external program speed of 100. The following speeds were used: low (30% of the maximum speed), medium (60% of the maximum speed) and high (90% of the maximum speed).

Percent of range in each axis.—The maximum range of motion for each of the axes was as follows: Joint 1: 320 degrees (waist), Joint 2: 250 degrees (shoulder), Joint 3: 270 degrees (elbow), Joint 4: 280 degrees (wrist 1), Joint 5: 200 degrees (wrist 2) and Joint 6: 520 degrees (wrist 3). The following ranges of motion were used: low (10% of the total range), medium (30% of the total range) and high (50% of the total range). The three ranges of the total motion used in this study are given in Table 1. The 50% axis movement was not exceeded because the return approach of the robot would have been unpredictable.

The robot was operated for a 15 minute warm up period before the data gathering began. The point called GAUGE to which the end effector was programmed to return was located near one of the extreme points of the axis system. This extreme point was determined by rotating joints 1, 3 and 5 of the robot the maximum amount in the negative direction and joints 2, 4 and 6 the maximum in the positive direction. The fixture with the three gauges was located at the point called GAUGE and contact was made with the tooling ball to accurately zero the three gauges. The PUMA 560 Victor Assembly Language was used to create a program that drove the end effector to one of the three locations determined by the chosen values for the variable, amount of axis movement, and returned it to the point GAUGE. This movement was repeated ten times for each of the twenty-seven combinations for levels of speed, weight and amount of axis movement. The radial error

Table 1. Ranges of motion used for each of the six axes for each of the three levels of axis movement.

Low (10%)	Medium (30%)	High (50%)
Joint 1: 32 degrees	Joint 1: 96 degrees	Joint 1: 160 degrees
Joint 2: 25 degrees	Joint 2: 75 degrees	Joint 2: 125 degrees
Joint 3: 27 degrees	Joint 3: 81 degrees	Joint 3: 135 degrees
Joint 4: 28 degrees	Joint 4: 84 degrees	Joint 4: 140 degrees
Joint 5: 20 degrees	Joint 5: 60 degrees	Joint 5: 100 degrees
Joint 6: 52 degrees	Joint 6: 156 degrees	Joint 6: 260 degrees

was measured each time the tooling ball returned to the point GAUGE. The total of 270 data measurements met the minimum for the twenty-seven factor level combinations according to the ANSI/RIA R15.02-2 standard (ANSI 1992).

RESULTS AND DISCUSSION

There were 10 measurements taken at each of the 27 factor level combinations. Therefore, the experiment is considered a full-factorial experiment with 10 replications. The response variable was the radial distance R from the point gauge to the location of the center of the tooling ball. This distance was computed from the errors in the X, Y and Z directions by $R = (X^2 + Y^2 + Z^2)^{1/2}$. After the experiment was designed and the 270 data points were obtained, data analysis was performed to determine if the three variables used in the experiment were all significant in determining the mean of error R. The analysis of the data using the Minitab software package yielded the main effects plots shown in Figure 1. These main effects plots indicate that each of the three variables was significant in determining the mean error. In general, the mean error was increased when any of the variables were changed from their medium or zero setting which indicated a quadratic relationship. Further evidence of the influence of the variables can be seen in Figure 2 which shows a graph of the error data in groups of ten replicates. This graph clearly indicates that the replicates produced tightly grouped errors but changes in levels of the three factors produced large changes in the magnitudes of the errors. Much of the variability in the values of the errors reflects changes in the factor levels. In order

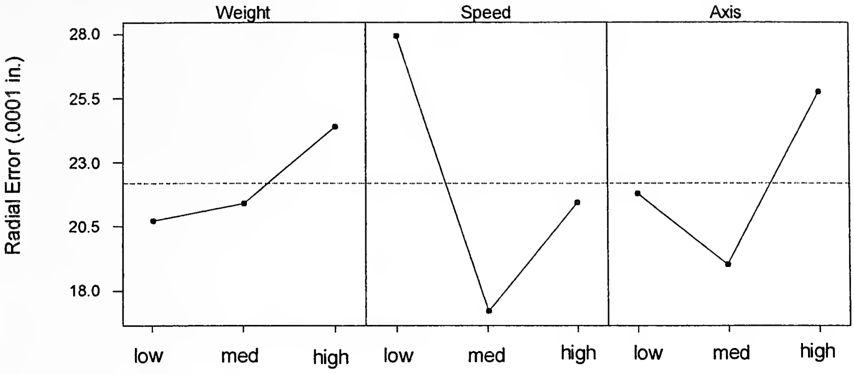

Figure 1. Main Effects Plot for R. The mean radial error is given as a function of each of the three factors at three levels as used in the study.

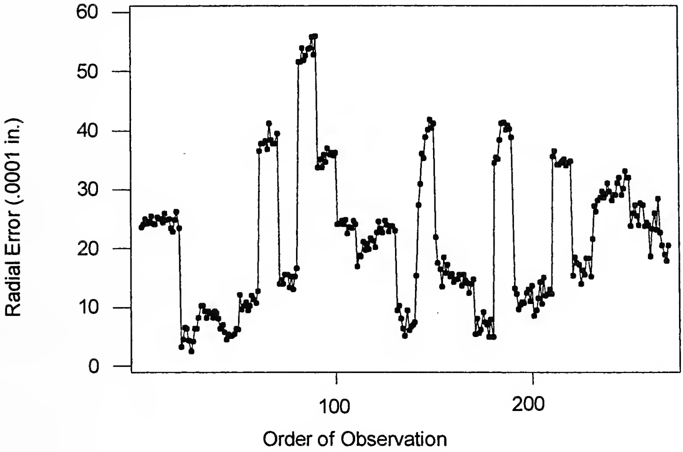

Figure 2. Radial Errors in Replicate Groups. The factor levels were changed after each group of ten observations. The data represent 270 observations with 27 different factor level combinations.

to get to the component of the data that reflects the repeatability of the robot, regression techniques with a linear model were used to remove the variation due to changes in factor levels. Figure 3 reveals the distribution of the random components of the data that determines the repeatability characteristic of the robot. This graph indicates an approximately normally distributed random pattern of error variation about the mean for the particular factor level combination at which the

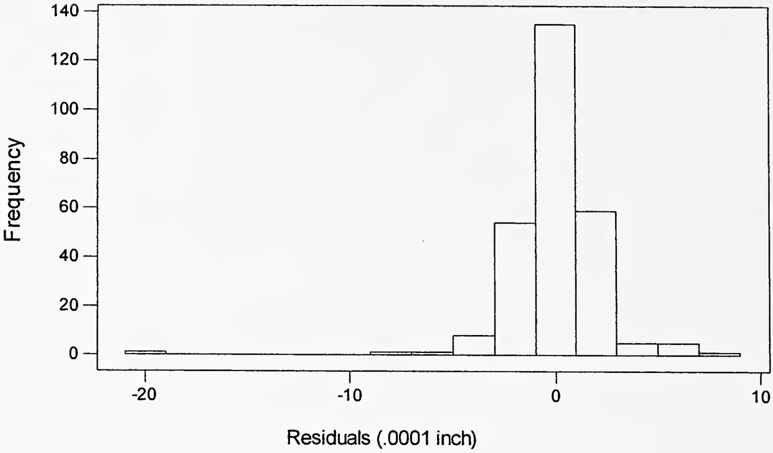

Figure 3. Histogram of Residuals Errors. Residual errors were calculated by subtracting the predicted radial error or accuracy from each measured radial error.

readings were taken. The computations in the analysis of variance (*ANOVA*) and the linear regression yielded the following equation to predict the accuracy:

$$RMEAN(W,S,A) = 11.8 - 3.25\,S + 1.44\,A + 1.85\,W - 3.32\,W{*}S$$
$$- 3.02\,W{*}A + 4.85\,S{*}A + 2.23\,W^2 + 8.59\,S^2 + 4.21\,A^2$$

Where: W = weight, S = speed and A = percent of axis movement.

The computations confirmed that the three factors, as well as their interactions, are statistically significant ($P < 0.05$) in the mean of the radial error values. Analysis of variance (*ANOVA*) computations produced a computed value of 98.4 for the variance of the random component of the radial error values. The square root of the variance yields the standard deviation of the random component to be 9.9. The repeatability of a robot was defined to be three times the standard deviation of the random component of the radial error. Therefore, the estimate for the repeatability of the Puma 560 turns out to be 29.7. Since measurements were in 0.0001 inch units, the repeatability estimate would be stated as 0.00297 inch. The estimate is somewhat smaller than the ±0.004 inch specified by the manufacturer. If regression techniques had not been used to remove the variability due to the changes in the factor levels, the standard deviation of the raw data would be 12.12. This standard deviation yields 0.001212 when the units are changed to inches and a corresponding repeatability estimate of 0.0036 inch. When rounded to the nearest thousandth of an inch, this estimate agrees with the manufacturer's estimate.

The adequacy of such a model is usually judged by R^2, the coefficient of determination, because it gives the fraction of the total variation in the radial error data explained by the model. This model developed for predicting the accuracy of the robot had an R^2 value of 35.2%. The statistical analysis clearly indicates that all three factors, as well as their interactions, affect the accuracy of the robot. However, the relationship between these factors and the accuracy is such that the standard linear regression techniques will not produce models which account for more than approximately 35% of the radial error variability, leaving approximately 65% of the radial error variability due to repeatability. When using a robot, the accuracy of the robot at a particular setting of the parameters can be determined by the regression model and adjustments can be made to compensate for the predicted mean radial error. However, the portion of the radial error which is due to repeatability must be tolerated without recourse. Manufacturers should therefore concentrate on giving more information about the accuracy of a robot. Since they have extensive test data for each model of robot, the manufacturer could provide a linear model for the purposes of predicting accuracy of the robot as well as an estimate of the constant repeatability.

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HISTORICAL POPULATION DYNAMICS OF RED SNAPPER (*LUTJANUS CAMPECHANUS*) IN THE NORTHERN GULF OF MEXICO

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Abstract.—A total of 313 young-of-the-year red snapper (*Lutjanus campechanus*) belonging to the 1999 year class were sampled from three geographic regions in the northern Gulf of Mexico and assayed for haplotype variation in mitochondrial (mt)DNA. Analysis of molecular variance revealed that only a small proportion (0.24%) of the genetic variance was distributed among regions; accordingly, the corresponding Φ_{ST} value did not differ significantly from zero. Exact tests of homogeneity of haplotype distributions also were non-significant. Tests for departure from a neutral Wright-Fisher model of genetic polymorphism, however, were significant, and a 'mismatch' distribution of nucleotide-site differences in mtDNA indicated that the departure from neutrality could be due to population expansion. Estimates of the time since expansion ranged from ≈270,000 to ≈420,000 years before present. The latter is consistent with the hypothesis that red snapper likely colonized the continental shelf in the northern Gulf following a glacial retreat. The observed departure from a neutral Wright-Fisher model also may suggest that insufficient time has lapsed for red snapper in the northern Gulf to attain equilibrium between mutation and genetic drift. However, the temporal signature provided by the 'mismatch' distribution is far older than the last glacial retreat which began ≈18,000 years ago. If the departure from neutrality reflects events occurring after the last glacial retreat, tests of present-day population or stock structure may well be compromised. The same may be true for other marine fish species in the northern Gulf.

Red snapper (*Lutjanus campechanus*) is an important, highly exploited marine fish distributed primarily along the continental shelf in the Gulf of Mexico from the Yucatan Peninsula in Mexico to the northeastern Florida coast (Hoese & Moore 1998). Although the species has provided an important fishery since the early 1900s, red snapper in U.S. waters have declined by an estimated 90% since the 1970s (Goodyear & Phares 1990). Factors impacting red snapper abundance include overexploitation by directed commercial and recreational fisheries, juvenile mortality associated with bycatch in the shrimp fishery, and habitat change (Gallaway et al. 1999; Ortiz et al. 2000). Management of red snapper resources in U.S. waters is currently based on a unit stock hypothesis (GMFMC 1989). Whether red snapper in fact comprise a single stock across the northern Gulf, however, remains an issue. Separate management of regional stocks, if they exist, would be a desirable goal to avoid regional over-exploitation and to conserve adaptive genetic variation (Carvalho & Hauser 1995; Hauser & Ward 1998).

Previous genetic work generally has been consistent with the existence of a single stock of red snapper in the northern Gulf (Camper et al. 1993; Gold et al. 2001) and with the hypothesis that significant gene flow occurs at one or more life-history stages (Goodyear 1995; Gold & Richardson 1998a). The hypothesis of significant gene flow is not consistent with a number of tagging studies that have shown adult red snapper to be sedentary and exhibit high site fidelity (Szedlmayer & Shipp 1994; Szedlmayer 1997). However, Patterson et al. (2001) recently documented extensive movement of adult red snapper in the northeastern Gulf and suggested that movement of adults might be sufficient to facilitate mixing across the northern Gulf. A second hypothesis is that observed genetic homogeneity reflects historic rather than contemporary gene flow, and that present-day red snapper could be isolated yet have been in sufficient genetic contact in the past to remain genetically indistinguishable (Camper et al. 1993; Gold & Richardson 1998a). In such situations, populations may not have reached equilibrium between mutation and genetic drift, and if so, would be expected to depart from expectations of the neutral Wright-Fisher model of genetic polymorphism (Fu 1997).

This study examined the alternate hypothesis by assessing patterns of mitochondrial (mt)DNA variation among red snapper sampled from three geographic regions in the northern Gulf and asking whether mtDNA haplotype distributions deviated from those expected under mutation-drift equilibrium. Populations that are expanding or declining typically are not in mutation-drift equilibrium (Fu 1997), and in such situations may leave a characteristic 'mismatch' distribution signature (Rogers & Harpending 1992). Consequently, this study also examined the 'mismatch' distribution of nucleotide site differences in mtDNA between pairs of individuals in order to assess whether red snapper in the northern Gulf had expanded or declined demographically. Red snapper were likely precluded from occupying most of the contemporary continental shelf in the northern Gulf during Pleistocene glacial advance (Gold & Richardson 1998a), and colonization of shelf waters following glacial retreat could have generated conditions conducive to population expansion.

MATERIALS AND METHODS

Young-of-the-year red snapper were procured in the fall of 1999 during a demersal trawl survey of the northern Gulf carried out by the

National Marine Fisheries Service (NMFS). Individual fish were sampled from the catch of a 12 m shrimp-trawl net, frozen onboard and returned to College Station where tissues were removed and stored at -80°C. Specimens were obtained from different offshore localities corresponding to three geographic regions (Fig. 1) representing the northwestern Gulf (south Texas coast, 14 trawls, $n = 127$, range/trawl = 4-12, mode = 8), the northcentral Gulf (Louisiana coast, 14 trawls, $n = 123$, range/trawl = 1-20, mode = 10), and the northeastern Gulf (Mississippi-Alabama coast, 9 trawls, $n = 63$, range/trawl = 1-13, mode = 10). Genomic DNA was isolated from frozen tissues as described in Gold & Richardson (1991).

Assay of mtDNA employed single strand conformational polymorphism or SSCP (Orita et al. 1989). Regions within the NADH-4 (ND-4) and NADH-6 (ND-6) protein-coding genes were sequenced and the Lasergene software package *Primer Select* was used to design polymerase-chain-reaction (PCR) primers that amplified mtDNA fragments less than 250 base pairs (bp) in size. The fragments were 163 bp from ND-4 and 122 bp from ND-6. PCR primers (forward primer first, then reverse primer) were as follows: ND-4 (5' – CAAAACCTTAATCTTCTACAATGCT – 3'; 5' – CAGGGGGTCTGTTGCTAT – 3') and ND-6 (5' – CGAAGCGTCCCCCGACT – 3'; 5' – CGGTTGATGAACTAGGTGATTTTTC – 3'). PCR conditions followed those used for red snapper microsatellites (Gold et al. 2001), except that annealing was carried out at 58°C and both primers for each fragment amplified were radioactively labelled. Following PCR, 5μL of stop solution (95% formamide, 0.05% bromophenol blue and xylene cyanol, 10 mM NaOH) was added to 10μL of PCR product. This solution was heat denatured at 100°C for 10 min and then snap-chilled in ice water. Varying gel composition and electrophoresis conditions optimized resolution of electromorphs. Adequate resolution was provided by electrophoresing PCR products at 500 V for 16 h on 8% non-denaturing polyacrylamide gels (37.5:1 acrylamide:bis-acrylamide, 0.5X TBE), supplemented with 5.0% glycerol (4.0% for NADH6) and run in 0.5X TBE buffer. The ND-4 and ND-6 electromorphs were best resolved by electrophoresis at 12°C. Efficiency of SSCP procedures to identify sequence variants was assessed by sequencing multiple representatives of each electromorph and comparing patterns of sequence divergence among them. Representatives of each electromorph were run on subsequent SSCP gels as reference controls.

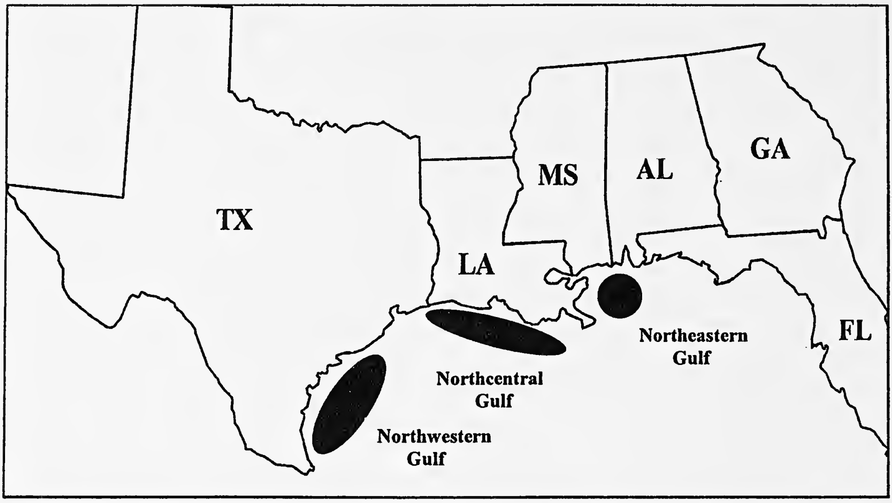

Figure 1. Collection localities of young-of-the-year red snapper (*Lutjanus campechanus*) from the northern Gulf of Mexico: northwestern Gulf (n = 127), northcentral Gulf (n = 123, and northeastern Gulf (n = 63).

MtDNA haplotype (nucleon) and nucleotide diversity were estimated after Nei (1987). The former represents the probability that any two individuals drawn at random will differ in mtDNA haplotype, whereas the latter represents the number of nucleotide differences per site between two randomly chosen sequences. Private haplotypes were tabulated and a V test (DeSalle et al. 1987) was used to test whether the proportion of private haplotypes differed significantly among regional samples. Homogeneity of mtDNA haplotype distributions among regions was assessed via analysis of molecular variance and exact tests (based on a Markov-chain procedure). For AMOVA, significance of the variance among samples and of Φ_{ST} was assessed by permutation (10,000 replicates). Both tests of homogeneity were carried out using ARLEQUIN (Schneider et al. 2000).

Deviation from mutation-drift equilibrium was assessed via Fu & Li's (1993) D^* and F^* and Fu's (1997) F_S measures of selective neutrality. Tests of significance of Fu and Li's D^* and F^* and Fu's F_S statistics were performed using DNASP (Rozas et al. 2003) and ARLEQUIN, respectively, and were based on 1,000 (D^* and F^*) and 10,000 (F_S) randomizations. Mismatch-distribution analysis (Rogers & Harpending

1992) was used to assess population expansion. As populations at mutation-drift equilibrium are expected to have ragged mismatch distributions (Rogers & Harpending 1992), the r measure of 'raggedness' (Harpending 1994) was calculated using ARLEQUIN; tests of $r = 0$ were carried out by parametric bootstrapping (10,000 replicates), also using ARLEQUIN.

RESULTS

Twelve electromorphs (A-L) of the 163 bp ND-4 fragment and fourteen electromorphs (A-N) of the 122 bp ND-6 fragment were identified via SSCP. Sequences of all electromorphs may be found in Table 1. All electromorphs of the ND-4 fragment differed by no more than a single nucleotide substitution from the most common electromorph (designated 'A'); for the ND-6 fragment, two electromorphs ('F' and 'G') differed by more than one nucleotide substitution from any other electromorph. Multiple representatives of each electromorph (both fragments) were sequenced but no variation within an electromorph type was detected.

A total of 32 composite mtDNA haplotypes were identified (Table 2). Haplotypes AA, BB, and AC were the most common, occurring at frequencies within regions of >0.300 (AA), 0.190 – 0.331 (BB), and 0.134 – 0.238 (AC). Twenty-one private haplotypes were observed; the number of private haplotypes per regional locality was 8 (Texas), 10 (Louisiana), and 3 (Mississippi/Alabama). None of the private alleles occurred at a frequency greater than 0.017, and the proportion of private haplotypes did not differ significantly among regions ($V_{[2]} = 0.657$, $P > 0.05$). Nucleon and nucleotide diversities among regions were 0.770 (Texas), 0.776 (Louisiana), and 0.798 (Mississippi/Alabama), and 0.006 (Texas), 0.007 (Louisiana), and 0.006 (Mississippi/Alabama), respectively.

Analysis of molecular variance revealed that only 0.24% of the molecular variation was distributed among samples rather than within samples; the Φ_{ST} value of 0.002 did not differ significantly ($P = 0.253$) from zero. An exact test of homogeneity in mtDNA haplotype distribution among regions also was non-significant ($P = 0.307$). Given the absence of heterogeneity in the distribution of mtDNA haplotypes among samples, all mtDNA haplotypes were pooled into a single sample for all subsequent analysis.

Table 1. Sequence electromorphs of NADH-4 and NADH-6 (mitochondrial DNA haplotypes) identified from red snapper (*Lutjanus campechanus*). Sequences are from the light strand of the molecule and are listed in the 5' to 3' direction. Note that NADH-6 is encoded on the heavy strand (i.e., codon positions would be reversed).

NADH4

Haplotype A	AAAAATCCTAATTCCAACCCTAATGCTCGTCCCAACAACTTGGCTGACCCCCGCCAAATGACTCTGACCTACAGCCCTTCTA
Haplotype B	....C...
Haplotype C	....
Haplotype D	....
Haplotype E	....G...............
Haplotype F	....T.................................
Haplotype G	....T..............................
Haplotype H	....
Haplotype I	....A.......................................
Haplotype J	....A........
Haplotype K	.....................G..
Haplotype L	....

Haplotype A	CACAGCCTAGTAATTGCACTTGCTAGCCTCACCTGATTGAAAAACCTCTCAGAAACAGGCTGGTCCTGCCTAAACCCCTAC
Haplotype B	....
Haplotype C	....G.......
Haplotype D	........T..
Haplotype E	....
Haplotype F	....
Haplotype G	....
Haplotype H	......................................A..
Haplotype I	....
Haplotype J	....
Haplotype K	....
Haplotype L	.....................A...

Table 1. Cont.

NADH6

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Haplotype A   CAACCCCCGTGTCAACTCCAGCACTACAAACAAAGTAAGTAAAAGAACTCATGCACTAATCAC
Haplotype B   ...............................................................
Haplotype C   ..G.................A..........................................
Haplotype D   ...............................................................
Haplotype E   ..G............................................................
Haplotype F   ...............T....A..........................................
Haplotype G   ....................A..........................................
Haplotype H   ...............................................................
Haplotype I   ...............................................................
Haplotype J   ...............................................................
Haplotype K   ....................A..........................................
Haplotype L   ....................A......G...................................
Haplotype M   ..G............................................................
Haplotype N   ..G.................................... .......................

Haplotype A   TAGTATCCCGCCCCCTAATGAGTACATCAACGCAACGCCCCCAATATCCCCCCGAAGCGT
Haplotype B   ...................................................G........
Haplotype C   ............................................................
Haplotype D   ..........................................................A.
Haplotype E   ............................................................
Haplotype F   ............................................................
Haplotype G   .....................A.......G..............................
Haplotype H   .........A..................................................
Haplotype I   .................................................G..........
Haplotype J   ..........................................G.................
Haplotype K   ................................................T...........
Haplotype L   ............................................................
Haplotype M   .................G..........................................
Haplotype N   ..A.........................................................
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Table 2. Frequencies of mitochondrial (mt)DNA haplotypes from age 0-1 red snapper (*Lutjanus campechanus*) sampled from three regions in the northern Gulf of Mexico. Sample region and number of individuals are northwestern Gulf (TX, n = 127), northcentral Gulf (LA, n = 123), and northeastern Gulf (MS-AL, n = 63). First letter (A-L) represents sequence eletromorphs at ND-4; second letter (A-N) represents sequence electromorphs at ND-6. Electromorph sequences may be found in Table 1.

MtDNA haplotype	TX	LA	MS-AL	MtDNA haplotype	TX	LA	MS-AL
AA	0.306	0.328	0.333	AJ		0.008	
BB	0.331	0.319	0.190	AK	0.008		
AC	0.165	0.134	0.238	AL		0.008	
AB	0.066	0.017	0.079	AM	0.008		
BA	0.008	0.017	0.048	BH	0.008		
AD	0.008	0.017	0.032	BN		0.008	
AE	0.016	0.017		CC			0.016
CA	0.008	0.017	0.016	FC	0.008		
AF	0.008	0.008		GC		0.008	
AG		0.008	0.016	GH		0.008	
AH		0.008	0.016	HA	0.008		
BC	0.016			IA	0.008		
BD	0.016			IC		0.008	
DA		0.017		JF		0.008	
EA		0.017		KA		0.008	
AI		0.008		LA			0.016

Fu & Li's (1993) D^* and F^* and Fu's (1997) F_S measures of selective neutrality were negative and significant for the pooled samples (D^* = -2.85, P = 0.019; F^* = -2.73, P = 0.007; F_S = -22.59, P = 0.000), consistent with demographic growth of a population (Fu 1997). Population growth (expansion) also was indicated by the unimodal mismatch distribution (Fig. 2) and by Harpending's (1994) raggedness index (r) which was non-significant (r = 0.107, P = 0.070). The time at which demographic expansion in red snapper might have occurred was estimated via the relationship $\tau = 2ut$ (Rogers & Harpending 1992). The value τ is the crest or peak of a unimodal mismatch distribution (measured in units of $1/2u$ generations), u is the mutation rate/generation of the region under study, and t is time in generations. The estimate of τ (2.412) was obtained from ARLEQUIN; u was estimated as the product of $m_T\mu$, where m_T is the number of nucleotides assayed (285) and μ is an estimate of the mutation rate per nucleotide. For estimate(s) of μ, the molecular-clock calibrations for mitochondrial protein-coding genes developed by Bermingham et al. (1997) were used and employed two rates (1.0%/10^6 yr and 1.5%/10^6 yr) for the (combined) ND-4 and ND-6 sequences from red snapper. For generation time, 15 and 20 years were used, framing the hypothesized generation time in red snapper of 17-19 years (J. Cowan, Louisiana State University, pers. comm.). Estimates

Figure 2. Mismatch distribution observed for mitochondrial DNA sequences (haplotypes) of young-of-the-year red snapper (*Lutjanus campechanus*) from the northern Gulf of Mexico. Bars represent observed frequency of differences between sequences; line represents the expected distribution assuming demographic expansion.

of u ranged from 1.5 x 10^{-7}/generation (μ = 1.0%/10^6 yr, 15 yr/generation) to 3.0 x 10^{-7}/generation (μ = 1.5%/10^6 yr, 20 yr/generation). Estimates of the time when demographic expansion in red snapper could have occurred ranged from ≈200,000 yr (u = 3.0 x 10^7/generation) to ≈540,000 yr (u = 1.5 x 10^7/generation). Despite uncertainties surrounding appropriateness of the molecular clock calibrations (Martin & Palumbi 1993; Rand 1994), and issues with use of pairwise-difference parameters such as τ (Felsenstein 1992), estimates of the time since demographic expansion in red snapper fit well within the Pleistocene epoch.

DISCUSSION

The observed homogeneity of mtDNA-SSCP haplotype frequencies among sample localities is consistent with the hypothesis that red snapper constitute a single stock in the northern Gulf. Similar findings were reported by Camper et al. (1993) based on restriction-site analysis of whole mtDNA and by Gold et al. (2001) based on analysis of microsatellites. Because genetic homogeneity typically implies sufficient gene flow to offset genetic divergence, continuous movement of red snapper at various life-history stages has been hypothesized (Goodyear 1995; Gold & Richardson 1998a; Patterson et al. 2001).

The significant departure of mtDNA variation from expectations of the neutral Wright-Fisher model of genetic polymorphism indicates that red snapper in the northern Gulf have not attained equilibrium between mutation and genetic drift. Moreover, the negative values for the 'neutrality' indices, particularly Fu's (1997) F_S index, suggest that the departure from neutrality stems from population growth. However, in addition to population growth, the D^* and F^* indices of Fu and Li (1993) and the F_S index of Fu (1997) also can signify either background selection or genetic hitchhiking, respectively (Fu 1997). Neither seems plausible in this case, in part because data are from mtDNA which is inherited as a single gene and independently from all nuclear genes, and in part because the mismatch distribution and Harpending's (1994) raggedness index were consistent with the hypothesis of historical population expansion. In addition, because red snapper were precluded from occupying much of the contemporary continental shelf in the Gulf when sea levels during Pleistocene glaciations were at least 100 m lower than they are today (CLIMAP 1976; Rezak et al. 1985), colonization of shelf waters and opening of favourable habitat following glacial retreat would be expected to generate conditions conducive to population expansion. This scenario is consistent with the estimated time of ≈200,000 – 540,000 years ago, given that the Pleistocene Epoch began approximately 1.8 million years ago (http://vulcan.wr.usgs.gov/Glossary/geo_time_scale.html).

Camper et al. (1993) and Gold et al. (2001) suggested that the genetic homogeneity observed among present-day red snapper in the northern Gulf might reflect historical rather than current gene flow. Briefly, genetic homogeneity among putatively isolated, present-day populations could be sustained provided there has been both insufficient time since colonization of continental-shelf waters and sufficiently large effective population sizes such that allele frequency differences arising via mutation have not reached mutation-drift equilibrium. However, the time since expansion indicated from the mismatch distribution (≈200,000 – 450,000 years ago) would seem too long for genetic divergence not to have arisen, assuming there has been no gene flow among localities and that effective population sizes are even one-tenth to one-hundredth of the current estimated census size of 7 – 20 million individuals. Unfortunately, estimating approximately how long it would take for genetic divergence to arise in this situation is problematic, given the absence of estimates of the effective (female) size of red snapper populations in the northern Gulf and the possibly unrealistic assumptions that red snapper form 'idealized' populations that exhibit an infiniteisland model of population structure. On the other hand, the last glacial retreat and the (re)opening of the continental shelf in the northern Gulf was only within the last 18,000 years (Rezak et al. 1985), a time period that is potentially too short for genetic divergence to occur if effective (female) sizes are only 1-2 orders of magnitude smaller than current census size and particularly if there is periodic gene flow among (semi-) isolated stocks.

There are a number of caveats to the above inferences. The first is that immigration of rare, genetically distinct mtDNA haplotypes also could generate negative D^*, F^*, and F_s values (Skibinski 2000). However, such immigration would be expected to lead to multimodal mismatch distributions (Marjoram & Donelley 1994), unlike the unimodal distributions observed here. A second caveat is that declining rather than expanding populations also can produce unimodal mismatch distributions. However, the 'wave' of a unimodal distribution of a declining population is expected to have an extremely steep leading edge, often with several secondary peaks that have large values (Rogers & Harpending 1992), a pattern not observed in the mismatch distribution generated from mtDNA sequences. Finally, the tests of neutrality may not necessarily measure the same temporal period as the mismatch distribution. The latter indicated a period of population expansion that occurred between ≈200,000 and 450,000 years ago, whereas the tests of neutrality could reflect an expansion dating to the last glacial retreat. At present, there is no way to distinguish among these alternatives.

Assuming red snapper in the northern Gulf deviate from mutation-drift equilibrium because of demographic expansion following the last glacial retreat, the question arises as to how prevalent are the same genetic patterns and demographic histories in other marine fishes in the northern Gulf. Grant & Bowen (1998) hypothesized that the combination of high haplotype diversity and low nucleotide diversity for mtDNA was indicative of a population bottleneck followed by rapid growth (their Category 2), and assigned two species that are common in the northern Gulf (red drum, *Sciaenops ocellatus*, and greater amberjack, *Seriola dumerili*) to this category. They erroneously assigned red snapper to Category 1 (low haplotype diversity and low nucleotide diversity) based on an error in reading Table 3 in Camper et al. (1993). Given the range of haplotype (0.770 – 0.798) and nucleotide (0.006 – 0.007) diversity found here, red snapper clearly belong in Category 2. A review of the literature reveals that many other fishes in the northern Gulf also appear to belong to Grant and Bowen's Category 2: Gulf toadfish, *Opsanus beta* (cf. Avise et al. 1987); Spanish sardine, *Sardinella aurita* (cf. Tringali & Wilson 1993); common snook, *Centropomus undecimalis* (cf. Tringali & Bert 1996), and black drum, *Pogonias chromis*, spotted seatrout, *Cynoscion nebulosus*, and king mackerel, *Scomberomorus cavalla* (synopsized in Gold & Richardson 1998b). Analysis of selective neutrality and of mismatch distributions of mtDNA datasets may demonstrate that these species also have undergone demographic expansions that could be dated approximately to changes in habitat availability during or following Pleistocene glaciation. Consequently, it may be that the (spatial) genetic homogeneity observed for many fishes in the northern Gulf of Mexico owes more to historical than contemporary gene flow, and that stocks meriting independent management may have gone unnoticed. A final important point to note that these current results do not necessarily reflect contemporary trends or contradict the documented decline of present-day red snapper stocks (Goodyear & Phares 1990), as evidence of historic demographic expansion is not necessarily affected by even severe bottlenecks that occur subsequent to population expansion (Rogers 1995; Lavery et al. 1996).

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GENERAL NOTES

NOTES ON REPRODUCTION IN THE FALSE CORAL SNAKES, *ERYTHROLAMPRUS BIZONA* AND *ERYTHROLAMPRUS MIMUS* (SERPENTES: COLUBRIDAE) FROM COSTA RICA

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Erythrolamprus bizona ranges from Costa Rica, south to Colombia and northern Venezuela and occurs from 8-1450 m in Costa Rica; *Erythrolamprus mimus* ranges from Honduras through Panama, western Colombia, Ecuador and northwestern Venezuela and occurs from 1-1200 m in Costa Rica (Savage 2002). Both are uncommon diurnal, secretive snakes that are oviparous (Savage 2002). The purpose of this note is to provide information on reproduction from a histological examination of gonadal material from museum specimens.

A sample of 40 specimens of *E. bizona* (females $n = 25$, mean snout-vent length [SVL] = 702 mm ± 83 *SD*, range = 545-835 mm; males $n = 15$, SVL = 614 mm ± 54 *SD*, range = 535-715 mm) and a sample of 13 specimens of *E. mimus* (females $n = 7$, SVL = 557 mm ± 37 *SD*, range = 504-615 mm; males $n = 6$, SVL = 482 mm ± 105 *SD*, range = 288-553 mm) from Costa Rica were examined from the herpetology collection of the Natural History Museum of Los Angeles County, Los Angeles (LACM). *Erythrolamprus bizona* were collected 1959-1980; *E. mimus* were collected 1966-1982. Counts were made of enlarged ovarian follicles ($>$ 12 mm length) or oviductal eggs. The left testis, vas deferens and a portion of the kidney were removed from males and the left ovary was removed from females for histological examination. Tissues were embedded in paraffin and sectioned at 5μm. Slides were stained with Harris' hematoxylin followed by eosin counterstain. Histological slides were examined to determine the stage of the testicular cycle and for the presence of yolk deposition (secondary vitellogenesis *sensu* Aldridge 1979). Number of tissues histologically examined by species were: *E. bizona* testis = 15, vas deferens = 15, kidney = 15, ovary = 12; *E. mimus* testis = 6, vas deferens = 6, kidney 6, ovary = 4. Follicles in advanced stages of yolk deposition or oviductal eggs were counted, but not histologically examined. An unpaired *t*-test was used to compare body sizes of male and female *E. bizona* samples.

Material examined.—The following specimens of *Erythrolamprus bizona* were examined by Costa Rica province: ALAJUELA (LACM 145932, 150656), CARTAGO (LACM 145843, 145847, 145954, 147512, 150643, 150644, 150650-150653, 150657-150660, 150703, 150706-150708, 150710), GUANACASTE (LACM 150654), PUNTARENAS (LACM 145792, 150704), SAN JOSÉ (LACM 67258, 145549, 145785, 145786, 145791, 145845, 145846, 145851, 145933, 145934, 145977, 147510, 150641, 150655, 150705, 150711). The following specimens of *Erythrolamprus mimus* were examined by Costa Rica province: ALAJUELA (LACM 150714, 150715, 150723, 150725, 150728), HEREDIA (LACM 150716, 150717, 150719), LIMÓN (LACM 150720), PUNTARENAS (LACM 150718, 150724), PROVINCE DATA MISSING (LACM 150721, 150722).

All testes examined from *E. bizona* and *E. mimus* were undergoing spermiogenesis (= sperm formation) with metamorphosing spermatids and sperm present. The following numbers of males were undergoing spermiogenesis: *E. bizona* February (1), April (1), June (2), July (1), August (1), September (1), October (5), November (1), December (2); *E. mimus* March (3), October (1), December (1). One *E. mimus* male (LACM 150728, SVL 288 mm) from February exhibited testicular recrudescence with spermatogonia and primary spermatocytes present. The size at which this snake would have undergone spermiogenesis is unknown. All vasa deferentia contained sperm and all kidney sexual segments from *E. bizona* and *E. mimus* were enlarged and contained secretory granules. Mating usually coincides with enlargement of the kidney sexual segments (Saint Girons 1982). The smallest *E. bizona* male to undergo spermiogenesis (LACM 150659) measured 535 mm SVL; the smallest *E. mimus* male to undergo spermiogenesis (LACM 150720) measured 432 mm SVL. It will be necessary to examine additional males to ascertain the minimum sizes at which *E. bizona* and *E. mimus* begin sperm formation.

Female *E. bizona* were significantly larger than males ($t = 3.67$, $df = 38$, $P < 0.01$). Samples of *E. mimus* were too small to make valid size comparisons between males and females. Females of *E. bizona* with oviductal eggs or enlarged follicles > 12 mm length were found in January-March and September-November (Table 1). One female from June (LACM 150650, SVL 777 mm) and one from October (LACM 150643, SVL 730 mm) were undergoing moderate yolk deposition and contained follicles 5-6 mm in length. It was not possible to predict the clutch size as other follicles might have undergone yolk deposition. Three females were undergoing early yolk deposition (secondary vitellogenesis *sensu* Aldridge 1979): June (LACM 145785, SVL = 821 mm),

Table 1. Monthly distribution of stages in the seasonal ovarian cycle of *Erythrolamprus bizona* from Costa Rica. Values shown are the numbers of females exhibiting each of the five conditions.

Month	*n*	Inactive	Early yolk deposition	Moderate yolk deposition*	Enlarged follicles > 12 mm length	Oviductal eggs
January	5	1	0	0	2	2
February	2	0	0	0	1	1
March	2	1	0	0	1	0
May	2	2	0	0	0	0
June	3	1	1	1	0	0
July	1	1	0	0	0	0
September	2	0	1	0	1	0
October	5	2	0	1	2	0
November	1	0	0	0	1	0
December	2	1	1	0	0	0

*follicles 5-6 mm length; one cannot predict final clutch size.

September (LACM 150653, SVL = 720 mm), December (LACM 150707, SVL = 645 mm). The smallest reproductively active female *E. bizona* (LACM 145932) measured 602 mm SVL (Table 2). The minimum size at which female *E. bizona* commence reproduction remains to be determined. Clutch sizes are listed in Table 2. Mean clutch size for 11 *E. bizona* clutches was 5.5 ± 1.8 *SD*, range = 3-9.

Mean clutch size for 4 *E. mimus* clutches was 3.8 ± 0.50 *SD*, range = 3-4. Body sizes, collection dates and locations are in Table 2. The smallest reproductively active female (oviductal eggs) measured 504 mm SVL (Table 2). The minimum size at which *E. mimus* females begin reproduction remains to be determined. One female from March (LACM 150718, SVL = 615 mm) and one female from October (LACM 150722, SVL = 575 mm) were not undergoing yolk deposition. One female *E. mimus* from December (LACM 150714, SVL = 563 mm) was undergoing early yolk deposition (secondary yolk deposition *sensu* Aldridge 1979).

There was no evidence that females of either *E. bizona* or *E. mimus* produce more than one clutch per year (i.e., oviductal eggs and yolk deposition in progress in the same female). However, in view of the extended period in which males undergo spermiogenesis and reproductively active females were found (Table 2), more than one clutch per year might be possible. *Erythrolamprus bizona* deposits its eggs in rotten logs or decomposed litter (Hardy & Boos 1995). Amaral (1978) reported the congener *Erythrolamprus aesculapii* from Brazil produced 6-9 eggs. Marques (1996) reported reproduction occurred throughout the year in *E. aesculapii* from southeastern Brazil and multiple clutches

Table 2. Clutch sizes for *Erythrolamprus bizona* and *E. mimus* (estimated from counts of enlarged follicles > 12 mm length or oviductal eggs*) from Costa Rica.

Date	SVL (mm)	Clutch size	Province	LACM #
		Erythrolamprus bizona		
3 January	827	6	Cartago	150651
24 January	760	5*	Puntarenas	145792
26 January	670	3*	San José	147510
27 January	700	6	Cartago	150708
1 February	835	9*	San José	145549
16 February	783	8	San José	145786
16 March	667	4	San José	150641
2 September	650	5	San José	145845
12 October	695	5	Cartago	145847
17 October	750	5*	Cartago	150706
24 November	602	4	Alajuela	145932
		Erythrolamprus mimus		
12 February	580	4*	Alajuela	150715
8 March	533	4*	Alajuela	150723
1 April	504	4*	Puntarenas	150724
6 Sept	531	3	Heredia	150719

were recorded from captive snakes. Clutch sizes ranged from one to eight eggs.

Additional monthly samples of *E. bizona* and *E. mimus* will need to be examined to obtain further information on the reproductive biology of these two species.

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A NEW DISTRIBUTION RECORD AND NOTES ON THE BIOLOGY OF THE BRITTLE STAR *OPHIACTIS SIMPLEX* (ECHINODERMATA: OPHIUROIDEA) IN TEXAS

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Brittle stars (Echinodermata: Ophiuroidea) are a common component of marine communities and often make up a significant portion of the biomass. Identification, however, can be problematic, particularly in the small fissiparous species. Fissiparity, asexual reproduction in which an individual divides in two and regenerates missing parts, occurs in 34 of the 2,000 species of brittle star (Emson & Wilkie 1980). One of these is *Ophiactis simplex*, an eastern Pacific species, with distribution from the Channel Islands to Panama and the Galapagos Islands (Neilsen 1932; Lonhart & Tupen 2001). Like other fissiparous brittle stars most specimens have six arms and are asymmetrical, with three long arms and three shorter arms. However, individuals with five and seven arms are not uncommon; the author has collected one with nine arms. One of the distinguishing characteristics of this species is the red tube feet. The red color is due to the presence of hemoglobin containing coelomocytes (RBCs) present in the water vascular system (Christensen 1999).

In late May 2001, five specimens of *O. simplex* were collected in a tide trap located on the research pier at the University of Texas Marine Science Institute, in Port Aransas, Texas. The specimens were found on algae caught in the net and were very small (disc diameter < 2 mm). Later that week approximately 200 specimens were collected from algae and other fouling material scraped from the rocks of the south jetty at Port Aransas. This represents a first report of this species along the Texas coast. Official counts were not made at this time. Voucher specimens were sent to Dr. Gordon Hendler at Museum of Natural History of Los Angeles for positive identification. Several subsequent collections have been made from the south jetty to determine habitat preference and population structure.

In January 2002, various species of algae, sponge, hydroid and tunicate colonies were scraped from the south jetty during an extremely low tide. Brittle stars were removed from the substrate, counted, and the volume of the substrate was estimated by measuring displacement volume. The brittle stars were sorted by disk diameter (large > 3 mm; medium 2-3 mm; small < 2 mm), regeneration state (recently split [2 or more arms < 2 mm], regenerating [2 or more arms of unequal length] and whole [all arms of equal length]) and redness of tube feet (bright red, medium red and colorless). The redness of the tube feet is a crude measure of the hematocrit (proportion of RBCs to water vascular system fluid). It is noted that individual hematocrit is variable in the Texas population: individuals possessing bright red tube feet have large numbers of RBCs in the water vascular system while others have colorless tube feet due to the scarcity of RBCs in the water vascular system. Actual hematocrits were not measured but were inferred from microscopic examination of several dissected individuals.

Collections were made again in June 2002, January and July 2003, primarily from colonies of the tunicate *Eudistoma carolinense*.

The densest aggregations of *Ophiactis simplex* were found in colonies of the sandy lobed tunicate, *Eudistoma carolinense* (75 individuals per 100 mL) (Table 1). Other substrates in which *O. simplex* were found included fire sponge (*Tedania ignis*), eroded sponge (*Haliclona loosanoffi*) and brown ribbed algae (*Dictyopteris* sp.) (Table 1). In January 2002, a total of 537 individuals was collected. Medium size individuals (2-3 mm disc diameter) were dominant (67%) and 58% of the individuals were nearly full or fully regenerated (Table 2). In contrast, the June 2002 collection yielded 414 individuals, 70.8% belonging to the small size class (< 2 mm disc diameter) and 82.6% of the individuals were in some stage of regeneration (Table 2). These animals were not sorted by tube feet color as significant mortality occurred before sorting. In July 2003, 229 individuals were collected, 88.2% belonging to the small size category and 83.4% were in some stage of regeneration.

Fission appears to be an important means of reproduction in the small and medium size classes, as most collected were in some stage of regeneration. Only two of the 27 large individuals collected were regenerating. The large size class also appears to be fairly uncommon; the largest individual collected had a disc diameter of 4.8 mm. Sexual reproduction also plays a role in this population of *O. simplex*. In the June 2002 collection, a large proportion (186 individuals) of the small size class was < 1 mm. The high number of small individuals indicates larval recruitment into the area (Mladenov & Emson 1984). Although

Table 1. List of substrates and densities from which *Ophiactis simplex* was collected. The different numbers associated with *Eudistoma carolinense* represent different colonies of the tunicate.

Species	Density
Tedania ignis	15/100 mL
Haliclona loosanoffi	17/100 mL
Dictyopteris sp.	8/100 mL
Eudistoma #1	35/100 mL
Eudistoma #2	41/100 mL
Eudistoma #3	79/100 mL
Eudistoma #4	28/100 mL
Eudistoma #5	61/100 mL
Eudistoma #6	25/100 mL

Table 2. Results of sorting the collections on the basis of size (small: disc diameter <2 mm; medium: disc diameter 2-3 mm; and large: disc diameter > 3 mm); regeneration state (recently split: half disc and 2 or more arms < 2 mm; regenerating: 2 or more arms of unequal length; and whole: all arms of equal length), and color of tube feet (indication of hematocrit).

	January, 2002	June, 2002	July, 2003
Size			
Small	157	293	202
Medium	359	117	25
Large	21	4	2
Regeneration state			
Recently split	34	67	31
Regenerating	191	275	160
Whole	312	72	38
Color of tube feet			
Bright red	199	*	94
Medium red	196	*	128
Colorless	142	*	7

* June, 2002, sample not sorted for color of tube feet due to significant mortality before sorting. The red color fades with death.

nothing has been reported on the reproductive periodicity of *O. simplex*, the appearance of so many extremely small individuals in the summer suggests an early spring spawn period. The July 2003 sample also yielded many very small animals but the exact numbers were not quantified.

There does not appear to be any relationship between regeneration state and color of tube feet. However, there does appear to be a weak relationship between size and color. There was only one large indi-

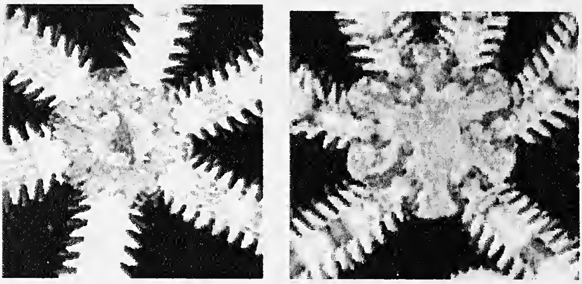

Figure 1. Aboral (surface) views of *Ophiactis savignyii* (left) and *Ophiactis simplex* (right).

vidual (disc diameter 3 mm) with colorless tube feet; all other large individuals possessed either medium or bright red tube feet. The larger individuals may be dependent upon hemoglobin for oxygen transport due to their reduced surface area to volume ratio whereas smaller individuals are likely small enough to obtain sufficient oxygen needed for aerobic metabolism by simple diffusion. Differences in the numbers of RBCs among individuals of the same size class may be due to oxygen availability in the microhabitat: those with bright red tube feet may inhabit areas with a lower oxygen tension than those with colorless tube feet. This possibility will be investigated further.

It is not known if this population of *O. simplex* is a recent introduction (e.g., through ballast water or drift algae) or if it has been present, but misidentified. A closely related species, *Ophiactis savignyii*, appears on collection lists for the area. Both are small and fissiparous, but *O. savignyii* does not possess hemoglobin. As mentioned earlier, not all specimens of the Texas population possess large amounts of hemoglobin and the red color disappears upon preservation with alcohol or formalin. Even with the small size, the two species are morphologically different. The radial shields (two at the base of each arm) of *O. savignyii* are very large; the length often exceeds half the disc radius, while those of *O. simplex* are much smaller (Hendler *et al.* 1995) (Figure 1). The arm spines are also markedly different: 4-5 long thin spines in *O. simplex* and 5-6 shorter, stubby spines in *O. savignyi*.

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FIRST DEFINITIVE RECORD OF MORE THAN TWO NESTING ATTEMPTS BY WILD WHITE-WINGED DOVES IN A SINGLE BREEDING SEASON

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The historical breeding range and recruitment of white-winged doves (*Zenaida asiatica*) in Texas was primarily restricted to a four-county region in the lower Rio Grande Valley (Cottam & Trefethen 1968). Recruitment in peripheral populations in adjacent south Texas counties and the Trans-Pecos region have been considered negligible (Gray 2002). In recent years, white-winged dove nesting chronology data have shown a geographic shift in nesting to include urban areas (Small & Waggerman 2000). This shift in nesting range occurred concurrent with a substantial northward range expansion of breeding white-winged doves, colonization of urban areas, and establishment of year-round populations over the last three decades (George et al. 1997; Schwertner et al. 2002).

As white-winged doves continue expanding their range and congregating in urban habitats, accurate measurement of annual recruitment is fundamental to understanding the ecology of this dynamic species. White-winged doves can nest twice in a single breeding season with speculation by some biologists of a greater number of nesting attempts (Cottam & Trefethen 1968, Alamia 1970, Swanson 1989). However, definitive records of more than two nesting attempts have not been documented prior to our account.

Two studies of breeding white-winged doves were conducted using surgically implanted radio transmitters. In 2000, breeding white-winged doves were monitored in Kingsville, Texas and in 2002-2003 in Waco, Texas. All white-winged doves were trapped locally in standard wire funnel traps (Reeves 1968) and implanted with subcutaneous radio transmitters in the field at trap sites (Small et al. 2004). In 2000, 40 doves (24 males, 16 females) were trapped and implanted between 19 May and 9 June. All doves were located to source once/week until onset of nesting. Nests were then monitored every four days using a mirror on an extendable pole and nest status recorded.

In 2002, 39 doves (16 males, 23 females) were trapped and implanted with transmitters in June and in 2003, 40 doves (17 males, 16 females, six unknown) were trapped and implanted in February and March. All doves were monitored as in 2000, for the life of the transmitter, up to but not exceeding 90 days.

During 2000, three male white-winged doves participated in three nesting attempts with unmarked females. Each attempt resulted in new nest construction. In each case, two nesting attempts proved successful with 1 failure. Young fledged on the first and second nesting but failed on the third for two nesting pairs. The other fledged young on the first and third attempts with the second failing. During 2002, one white-winged dove (sex unknown) made three nesting attempts. Two attempts fledged young, nests 1 and 2, with nest 3 failing. During 2003, one female white-winged dove made four nesting attempts with the first and fourth attempts fledging young. The second attempt resulted in nest

Table 1. Observations for an individual white-winged dove attempting four successive nestings.

	Nest				Tree		
Attempt	Date	Success	Height (m)	Distance from last nest (m)	Species	Height (m)	Same/ Different
1	04/08/03	2 fledged	2.32	NA	Pecan	6.67	NA
2	05/23/03	abandoned	2.90	7.0	Pecan	6.67	same
3	06/11/03	nest failed	8.06	7.0	Live Oak	16.64	different
4	06/18/03	2 fledged	2.33	7.0	Pecan	6.67	different

abandonment and the third nest failed.

In all multiple nesting attempts, no doves reused a nest. Doves built new nests either in the same tree or a nearby tree = 100 m from the old nest. Because of its uniqueness, additional information for the individual with four nesting attempts is presented (Table 1).

Although some anecdotal evidence of > two nesting attempts by white-winged doves exists, radio telemetric methodology allowed us to report the first definitive occurrence of > two nesting attempts. Whether this is a unique occurrence or a fundamental aspect of white-winged dove natural history is unknown. Because of the dynamic range expansion, urbanization, and proportional residency shifts of white-winged doves over the last 30 - 50 years, frequency of > two nesting attempts in historic populations will probably never be known.

The availability of anthropogenic food and water resources and habitat associated with urbanization have the potential to extend the breeding season (Hayslette & Hayslette 1999) which could represent a shift in the reproductive strategy for white-winged doves. During 2002, one pair of doves with radio transmitters pair bonded, but both batteries failed after 1 successful nesting. Consequently, the issue of monogamy in wild populations of white-winged doves remains unanswered in this study. Further research is fundamental to understanding the dynamics of multiple nesting, monogamy and an extended breeding season on recruitment.

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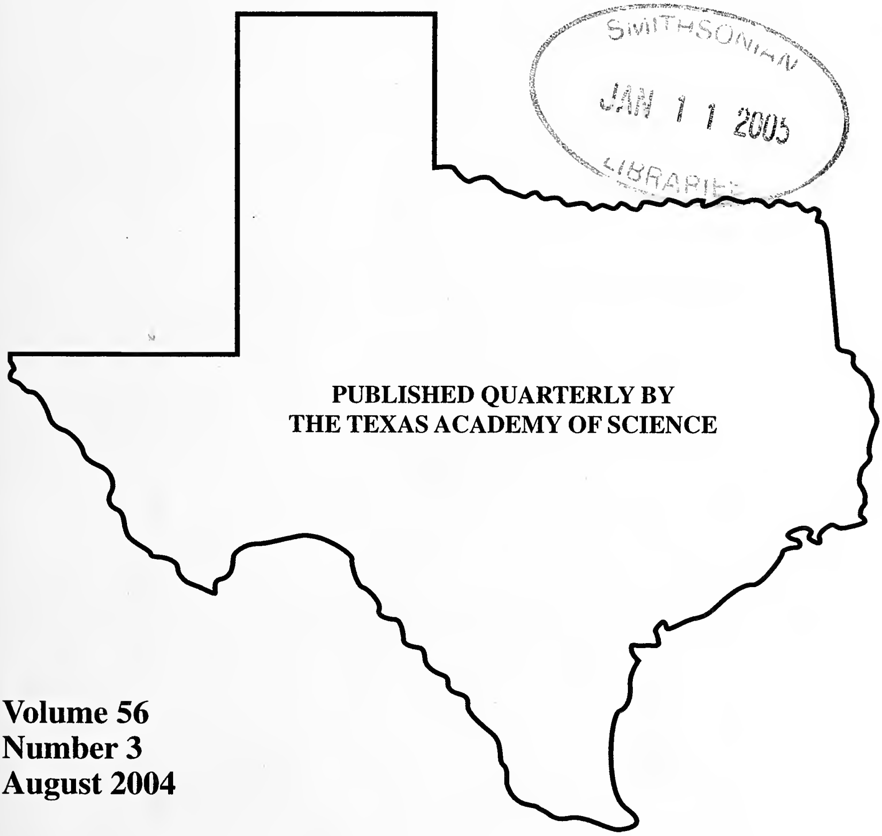

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OBSERVATIONS OF BIRD COMMUNITIES IN RELATION TO RESERVOIR IMPOUNDMENT

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Abstract.—This study describes trends in terrestrial avian communities in response to construction of Aquilla Lake in north-central Texas. Reservoir construction and filling resulted in substantial loss of area in each of four major habitat types. Pre-impoundment surveys began in 1979, with follow up post-impoundment surveys in 1984, 1987 and 1992. Mean bird density, species richness and species diversity were highest among all seasons during the pre-impoundment survey, but declined markedly by the first post-impoundment study. Similarity in bird species composition was greatest among the post-impoundment avian communities. Northern cardinal (*Cardinalis cardinalis*) and Carolina chickadee (*Poecile carolinensis*) were the two most common species encountered in all seasons across study phases. Comparisons with data from two adjacent North American Breeding Bird Survey routes suggest that declines among six species may have been related to reservoir construction. Over time, post-impoundment bird communities on Aquilla Lake had fewer bird numbers, had fewer bird species, and were more similar to one another in species composition.

Riparian habitats are productive, diverse and structurally complex habitats that support large aggregations of breeding and riparian dependent bird species (Carothers & Johnson 1975). These habitats also provide critical resources to more vertebrate species than any other habitat type, yet less than 2% of the United States (US) land area is comprised of this habitat type (Sedgwick & Knopf 1987; Douglas et al. 1992; Naiman et al. 1993). Further, > 89% of riparian habitat in the US has been lost over the last 200 years, primarily due to logging, agricultural practices and development (Douglas et al. 1992; Croonquist & Brooks 1993). The damming of stream and river systems for reservoir construction has also resulted in substantial loss of riparian habitats.

Reservoirs are created for a variety of uses that include flood control, recreation and municipal water supply. As human populations continue to grow, the demand for water resources will continue to increase with greater emphasis on reservoir construction to supply that need. In Texas, for example, there are currently 440 reservoirs with greater than 400 ha of conservation storage capacity; 211 of these have greater than 2,000 ha of conservation storage capacity (Texas Water Development

Board 2002). Construction of an additional eight major and 10 minor reservoirs has been recommended to meet the future water needs of a growing Texas population beyond 2002, as mandated by the state water plan (Texas Water Development Board 2002). Also, 33 sites uniquely suited for reservoir development have been identified for future development by water board planning groups. Reservoir construction can have negative impacts on habitat for terrestrial wildlife species. Impoundment of natural watercourses results in direct loss of species-rich riparian habitats, and fragmentation of remaining forest patches. The proposed construction of 44 reservoirs in Texas during the early 1990s, for example, would have directly impacted an estimated 344,399 ha of wildlife habitat (Frye & Curtis 1990).

Habitat loss and fragmentation effects on terrestrial bird communities have been well studied in numerous environments (Ambuel & Temple 1983; Terbourgh 1989; Hill & Hagen 1991; James et al. 1992; Sauer & Droege 1992; Andren 1994; Herkert 1994; Winter & Faaborg 1999; Coppedge et al. 2001). The impacts on terrestrial avian communities resulting from construction and subsequent filling of reservoirs have largely been ignored by avian ecologists. This is surprising in light of the many reservoirs that exist throughout the southern US, and Texas in particular. This study describes the changes in terrestrial avian communities in context to reservoir construction in north-central Texas over a 14 year time frame.

METHODS

Study area.—The project study site was located in Hill County, approximately 11.2 km southwest of Hillsboro, Texas. The project area was defined as all lands purchased in fee and/or easement necessary for reservoir construction, as well as all lands within the flood pool elevation of 169.5 m. The 4,133.2 ha study site was located within the Black-land Prairie and eastern Cross Timbers and Prairies vegetation zones (Gould 1975; Slack et al. 1996). The Blackland Prairie region has alkaline black clay soils with high organic content overlying parent Cretaceous limestone. Prior to agricultural conversion, the dominant herbaceous vegetation was little bluestem (*Schizachrium scoparium*); currently it is confined to small scattered areas in the eastern part of the county. The Eastern Cross Timbers consists of a belt of post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) extending from the Red River into southern Hill County. The terrain of the study site was nearly level to rolling, and was dissected by Aquilla, Little Aquilla and Hackberry Creeks. Impoundment of Aquilla Lake by the U.S. Army Corps of Engineers (USACOE) began on 29 April 1983 and reached conservation pool level (163.9 m) two years later on 21 March 1985. The dam site was located in Hill County (97°13'24"W, 31°054'44"N) on Aquilla Creek at river mile 23.6 (km 38).

Habitat mapping and bird surveys.—Major habitat types within the project boundaries were mapped and their post-impoundment areal changes quantified from color aerial photographs using ARCINFO Geographic Information System beginning with the pre-impoundment phase I (1979), and each post-impoundment phase: II (1984), III (1987), IV (1991). The avian community was surveyed using three 40 m wide belt transects established prior to lake construction; transects were placed in a manner that would sample the major habitat types in proximity to the projected reservoir basin. Each transect differed in length and sampled habitat types to varying degrees. Transect one was initially 3.7 km long, 37%, 53% and 9.9% of which was represented by forest parkland, old field and riparian woodland habitat types, respectively. Transect one was reduced in length by rising water levels to 2.8 km and 2.5 km in 1987 and 1984, respectively. Transect two was 2.8 km long, 97% of which was in the old field habitat type. Transect three was 1.7 km long and was comprised of 38% forest parkland, 16% riparian woodland and 46% old field habitat. Lengths of transect two and three were unaffected by the filling of the reservoir.

Initially, a transect was established in riparian woodland habitat off the reservoir acquisition site as a control to evaluate reservoir impacts. In the winter of 1984, this site was cleared and converted to tame pasture, negating its use as a true control; results from this transect are not reported in this study. To establish some context for interpreting reservoir effects, data from two North American Breeding Bird Survey (BBS) routes located near Aquilla Lake over the same time period (Sauer et al. 2001) was compared. Abundance data for the 11 most abundant species encountered during June surveys on Aquilla Lake were obtained from the Osage BBS route (TEX-050, 97°33'27"W, 31°22'23"N) and the Pidcoke BBS route (TEX-051, 97°52'29"W, 31°20'29"N), pooled (n = 27) and regressed against time (1979-1992). The hypothesis that the slope of the regression line (β_1) for each species did not differ using 95% confidence intervals (Johnson 1999) was tested. If a particular bird species declined on the study site post-impoundment and also was

Table 1. Area (ha) and percent change (%) over time of habitat types on Aquilla Lake reservoir site. Years correspond to pre-impoundment (1979-80), and post-impoundment I (1984-85), II (1987-88) and III (1991-92) surveys.

Habitat Type	1979-80	1984-85	%	1987-88	%	1991-92	%
Forest Parkland	428.8	331.8	-22.6	235.3	-29.0	235.3	0
Scrub/Shrub	484.6	29.3	-93.9	25.2	-14.0	25.2	0
Riparian Woodland	1633.8	614.3	-62.4	57.2	-90.7	57.2	0
Old-field [1]	735.5	660.4	-10.2	435.4	-34.0	435.4	0

[1] Includes area of crop, pasture and old-field habitats pre-impoundment.

declining on BBS routes for the same time frame, this would suggest that reservoir construction had little or no effect on the changing numbers for that species.

Transects were walked once per quarter during the first three hours of daylight. All birds seen within 20 m on either side of the transect line were identified and recorded. Each of the post-impoundment studies employed a different observer in conducting transect counts. Bird density was calculated seasonally on each transect by dividing the number of birds seen by the area covered (transect length x 40 m); transect density estimates were averaged to obtain a mean bird density (birds/ha ± SE) across the study area. Species richness (r), Simpson's D, Shannon's diversity (H') and Morisita's index of similarity (Krebs 1989) were computed seasonally for pre-impoundment and post-impoundment surveys to compare seasonal bird communities across all phases of this study.

RESULTS

Four major habitat types were classified from pre-impoundment aerial photographs: forest parkland, riparian woodland, scrub/shrub and old field. All four habitats types were reduced in area due to reservoir construction (Table 1). Riparian woodland was the largest habitat type prior to impoundment and experienced the most rapid rate of loss over the course of the study (Table 1).

Mean bird density and species richness was higher in the pre-impoundment phase across seasons than in all post-impoundment phases (Table 2); pre-impoundment bird densities were highest during fall and summer. Bird density then declined in all seasons (< 10 birds/ha) between the pre-impoundment and the first post-impoundment phase

Table 2. Species richness (r), Simpson's D (S[D]) and Shannon-Weiner H' (SW[H']) diversity values, and mean density (D, birds/ha) and standard error (SE) for land-bird communities by year and season on Aquilla Lake. Years correspond to pre-impoundment (1979-80), and post-impoundment I (1984-85), II (1987-88) and III (1991-92) surveys.

Season	Year	r	S(D)	SW(H')	D	D(SE)
Winter	1979-80	44	0.931	3.003	20.2	(6.1)
	1984-85	25	0.914	2.731	8.7	(2.4)
	1987-88	13	0.789	1.913	3.5	(0.9)
	1991-92	17	0.870	2.269	5.3	(1.7)
Spring	1979-80	45	0.918	2.987	24.7	(5.4)
	1984-85	17	0.858	2.252	6.3	(0.8)
	1987-88	15	0.891	2.309	2.4	(0.8)
	1991-92	17	0.915	2.504	2.8	(1.0)
Summer	1979-80	64	0.907	2.978	59.6	(9.8)
	1984-85	12	0.872	2.187	2.2	(1.1)
	1987-88	14	0.766	1.864	2.8	(0.5)
	1991-92	18	0.840	2.226	2.9	(0.7)
Fall	1979-80	84	0.907	3.037	77.4	(19.6)
	1984-85	14	0.851	2.137	2.8	(1.3)
	1987-88	11	0.783	1.865	2.6	(0.8)
	1991-92	11	0.868	2.113	2.1	(0.8)

(Table 2). Species richness values also declined > 50% across seasons between the pre-impoundment and first post-impoundment sampling periods (Table 2); pre-impoundment richness values were highest during winter and summer.

Morisita's index of similarity revealed a reduction in similarity between the pre-impoundment survey and all post-impoundment surveys during the fall and winter seasons (Table 3). Collectively, post-impoundment bird communities were most similar to the pre-impoundment values during the summer (Table 3). In all seasons but winter, there was greater similarity among post-impoundment surveys than between pre-impoundment and post-impoundment comparisons (Table 3). The similarity between pre-impoundment and post-impoundment bird communities exceeded 50% only in the summer survey periods.

Forty-eight percent (*n* = 19), 51% (*n* = 23), 54% (*n* = 23) and 79% (*n* = 66) of the birds recorded during the pre-impoundment surveys during winter, spring, summer and fall, respectively, were never recorded in the subsequent post-impoundment surveys. The two most abundant species encountered in all seasons and surveys were northern cardinal and Carolina chickadees; American robins and eastern meadowlarks were most abundant during the winter and spring surveys.

Table 3. Morisita's community similarity values of seasonal pre-impoundment and post-impoundment land bird communities over time on Aquilla Lake, Hill County, Texas. Years correspond to pre-impoundment (1979-80), post-impoundment I (1984-85), II (1987-88) and III (1991-92) surveys.

Season	Year	1984-85	1987-88	1991-92
Winter	1979-80	0.685	0.485	0.404
	1984-85		0.631	0.255
	1987-88			0.267
Spring	1979-80	0.332	0.385	0.339
	1984-85		0.667	0.648
	1987-88			0.674
Summer	1979-80	0.448	0.571	0.607
	1984-85		0.829	0.858
	1987-88			0.967
Fall	1979-80	0.310	0.269	0.224
	1984-85		0.514	0.505
	1987-88			0.843

Twenty-four species of neotropical migrants were observed during the summer pre-impoundment phase of the study. Yellow-billed cuckoos (*Coccyzus americanus*) and dickcissels (*Spiza americana*) were the most abundant neotropical migrants in all four phases of summer surveys, and both exhibited the most marked decline in post-impoundment surveys.

The 11 most abundant birds seen during summer surveys on Aquilla Lake included northern bobwhite (*Colinus virginianus*), northern cardinal, Carolina chickadee, yellow-billed cuckoo, dickcissel, killdeer (*Charadrius vociferus*), lark sparrow (*Chondestes grammacus*), eastern meadowlark, northern mockingbird (*Mimus polyglottos*), mourning dove and painted bunting (*Passerina ciris*). BBS data from the Osage and Pidcoke route were pooled for each of these species to achieve better representation of the area around Aquilla Lake. Confidence interval tests of $\beta_1 = 0$ for northern cardinal, Carolina chickadee, mourning dove, painted bunting, yellow-billed cuckoo and dickcissel showed no significant decline for the time frame of this study ($P > 0.05$, $n = 27$, $df = 25$). Negative trends in abundance were found for eastern meadow larks, northern bobwhite, killdeer, lark sparrows and northern mockingbirds ($P < 0.05$, $n = 27$, $df = 25$).

DISCUSSION

The decline of terrestrial birds in the Aquilla Lake area over the course of this study was apparent in density, species diversity and species richness values. The greatest reduction in bird abundance occurred between pre-impoundment and the first post-impoundment phase. Bird densities leveled off after Aquilla Lake reached conservation pool level in 1985. The decline in bird density was mirrored by declines in species richness and species diversity. Results from this study showed post-impoundment bird communities on Aquilla Lake had fewer bird numbers, had lower species diversity and richness, and were more similar to one another in species composition when compared to the pre-impoundment surveys.

Analysis of BBS route data suggest that there were changes among bird species at Aquilla Lake that were not occurring in the surrounding region. Northern cardinals and Carolina chickadees were the two most abundant residents during the pre-impoundment survey of 1980, and both declined to 5 and 16% of their pre-impoundment abundance, respectively, by 1984; this was somewhat surprising given that these two species were not habitat specialists or forest interior obligates. Indeed, the combined BBS data showed no significant trend in the abundance of these two species in the surrounding region for the time period of our study. Likewise, mourning doves, painted buntings, yellow-billed cuckoos and dickcissels showed no trend on BBS routes, but all declined on the Aquilla Lake study site.

The change in bird density coincided with the loss of habitat area on the Aquilla Lake site. This apparent cause and effect relationship has been documented by numerous studies of habitat fragmentation effects on bird communities (Forman et al. 1976; Galli et al. 1976; Whitcomb et al. 1977; Robbins 1980; Terbourgh 1989). Loss of habitat area alone, however, has not always explained downward trends in songbird populations (Ambuel & Temple 1983). Sauer & Droege (1992) reported that over the long term, more species of neotropical migrants were increasing than were decreasing with no association between short term declines and changes in forest acreage. James et al. (1992) also reported results that were not consistent with the view that neotropical migrant warblers occupying forest habitats were declining. Hill & Hagen (1991) analyzed population trends of North American birds and found that many species were declining, but that declines in the past 20 years might be in part a result of normal short-term population fluctuations.

Plant succession could also account for some of the change in abundance among species at Aquilla Lake, especially in the old-field and scrub/shrub habitat types. There was no active habitat management (e.g., prescribed fire) on the USACOE property surrounding Aquilla Lake. Over the course of this study, old-field and scrub/shrub habitats likely changed in floristics and structure with subsequent effects on the avian community. This might explain some of the declines seen in eastern meadowlarks, northern bobwhites and lark sparrows.

The ability to detect reservoir impacts was hampered by several factors. First, land use impacts on a control area off the reservoir site precluded direct evaluation of reservoir effects. A true control site would have been difficult to obtain for the length of the study period, since most of the surrounding property was privately owned and subjected to various agricultural land use practices; such practices did affect the initial control site early in this study. Second, direct cause and effect could not be made due to methodological differences between transect counts and BBS counts. The reason for using BBS data was to provide some context to the data, because published data from other reservoir construction projects does not exist. To that end, the use of BBS data provided tangential support of the results of this study regarding the impacts on bird communities from reservoir construction: some bird species declined on the reservoir site during the study period, but showed no such trend in the surrounding area.

Given that reservoir development will continue in order to provide for a growing Texas population, further research on existing and future reservoir sites would seem warranted. Existing reservoirs could provide opportunities to investigate long term effects of habitat loss and fragmentation on abundance, richness, diversity and the degree of species recovery over time; such data would be especially valuable where they exist in proximity to established BBS routes. New reservoir construction projects could offer opportunities to further quantify the immediate post construction impacts on richness, diversity and abundance of avian communities.

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SEASONAL AND ECOLOGICAL ASSOCIATIONS OF THE AVIFAUNA FROM SIERRA SAN ANTONIO-PEÑA NEVADA, ZARAGOZA, NUEVO LEÓN, MÉXICO.

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Abstract.—This study examined the avifauna of three vegetational communities of the Sierra San Antonio-Peña Nevada of northeastern México, from June 2001 to May 2002. A total of 1,084 individuals were recorded, comprising 83 species, 62 genera, 31 families and 9 orders. The ecological associations of the species were as follows: Pine 40; Pine-Oak 48; and Oak 58. The seasonal distribution of the species was: Spring 48; Summer 42; Fall 47; and Winter 40. Based on the Shannon's Diversity Index, the highest values were obtained for Oak Forest (H' =3.16) and for Spring (H' =3.26).

Resumen.—El presente estudio se realizó sobre la avifauna de tres comunidades vegetales de la Sierra San Antonio-Peña Nevada, de junio de 2001 a mayo de 2002. Se registraron 1, 084 individuos, correspondientes a 83 especies, 62 géneros, 31 familias y 9 órdenes. La distribución ecológica de las especies fue la siguiente: Bosque de Pino, 40; Bosque Mixto, 48; y Bosque de Encino, 58. En cuanto a la distribución estacional, se obtuvo: Primavera, 48 especies; Verano, 42; Otoño, 47; e Invierno, 40. Utilizando el Índice de Diversidad de Shannon se obtuvieron los valores más altos para el Bosque de Encino (H' =3.16) y para Primavera (H' =3.26).

Many avian studies in coniferous forests of North America have concluded that vegetation coverage or foliage is a factor that positively influences bird species presence, richness and abundance (Tatschl 1967; Balda 1969; Dickson & Segelquist 1979; Beedy 1981; Anderson et al. 1983; Bazakas 1996; Guzmán-Velasco 1998; García et al. 1998; Daniel & Flete 1999; Mills et al. 2000; Doherty & Grubb 2000; Latta et al. 2003). Also, in the South American Andes, the distribution of some species is apparently determined by the vegetation type (Terborgh 1971).

Avian communities are not static but change seasonally; in fact, bird assemblages in temperate regions are composed by permanent residents and winter and summer visitors that vary throughout the year (e.g., Hilden 1965; Anderson 1972). Several studies in North American forests have found differences in species richness, density and composition in different seasons and habitat types (Anderson et al. 1983; Avery & van Riper III 1989; Corcuera & Butterfield 1999; Latta et al. 2003).

In México, several researchers have established the ecological distribution of the avian communities of some elevated orographic formations, especially with respect to the effects of altitudinal gradients on bird species (Miller 1955; Morales-Pérez & Navarro-Sigüenza 1991; Navarro 1992; Winker 1992; García et al. 1998). Previous studies on birds diversity in Nuevo León are mainly inventories and generally the locality is not mentioned (Friedmann et al. 1950; Miller et al. 1957; Martín-del Campo 1959; Contreras-Balderas et al. 1995; Contreras-Balderas 1997; Howell & Webb 1995). Ecological aspects of the avifauna in the state are almost non-existent, however, Guzmán-Velasco's (1998) study on Cerro El Potosí and González-Iglesias' (2001) research on Sierra Picachos are an exception. This present effort is the first systematic study of the avian community of Sierra San Antonio-Peña Nevada in terms of species richness, abundance, and ecological and seasonal distribution.

STUDY SITE

The study area (23°52'12" to 23°40'12" N and 99°57'00" to 99°39'36" W) is located in the southeastern region of General Zaragoza municipality of Nuevo León. Its total area is approximately 209.57 km^2 and its elevation ranges from 2,200 - 3,400 m (INEGI 1986; Arriaga et al. 2000).

This mountainous area is also the second highest elevation of Nuevo León, exhibiting diverse vegetational communities that vary from chaparral (*Quercus*, *Dasilyrion*, *Agave*) to fir forests (*Abies-Pseudotsuga)*, including those specific to this study: Pine Forest (*Pinus*), Pine-Oak Forest (*Pinus-Quercus*) and Oak Forest (*Quercus*). It is situated in the Sierra Madre Oriental, but especially in the transition zone between the Neotropical and Neartic biogeographic regions, making this a natural ecotone. The Sierra Peña Nevada is also considered as a Prioritary Terrestrial Region for Conservation (Arriaga et al. 2000) and an Area of Importance for Birds Conservation in México (Arizmendi & Márquez 2000).

MATERIALS AND METHODS

The study site was visited monthly from April 1996 to May 2001. Each vegetation type was sampled once each season, using 18 point counts and 18 mist nets (distributed in 9 stations). Point counts followed

Table 1. List of species and their residency status: PR = Permanent resident; SR = Summer Resident; WR = Winter Resident; T = Transient; V = Vagrant; and * = Undetermined.

Species	Common Name (Spanish)	Common Name (English)	Residency
Coragyps atratus	Zopilote común	Black Vulture	PR
Cathartes aura	Zopilote aura	Turkey Vulture	PR
Buteo brachyurus	Aguililla cola corta	Short-tailed Hawk	PR
Buteo albonotatus	Aguililla aura	Zone-tailed Hawk	PR
Buteo jamaicensis	Aguililla cola roja	Red-tailed Hawk	PR
Patagioenas fasciata	Paloma de collar	Band-tailed Pigeon	PR
Zenaida macroura	Paloma huilota	Mourning Dove	PR
Otus flammeolus	Tecolote ojo oscuro	Flammulated Owl	SR
Megascops asio	Tecolote oriental	Eastern Screech-Owl	PR
Megascops trichopsis	Tecolote rítmico	Whiskered Screech-Owl	PR
Glaucidium gnoma	Tecolote serrano	Northern Pygmy-Owl	PR
Micrathene whitneyi	Tecolote enano	Elf Owl	T
Caprimulgus vociferus	Tapacamino cuerporrín-norteño	Whip-poor-will	PR
Hylocharis leucotis	Zafiro oreja blanca	White-eared Hummingbird	PR
Lampormis clemenciae	Colibrí garganta azul	Blue-throated Hummingbird	PR
Eugenes fulgens	Colibrí magnífico	Magnificent Hummingbird	PR
Selasphorus platycercus	Zumbador cola ancha	Broad-tailed Hummingbird	SR
Trogon mexicanus	Trogón mexicano	Mountain Trogon	PR
Melanerpes formicivorus	Carpintero bellotero	Acorn Woodpecker	PR
Picoides villosus	Carpintero velloso-mayor	Hairy Woodpecker	PR
Colaptes auratus	Carpintero de pechera	Northern Flicker	PR
Lepidocolaptes sp.	Trepatroncos	Woodcreeper	*
Contopus sp.	Pibí	Wood-Pewee	*
Empidonax flaviventris	Mosquero vientre amarillo	Yellow-bellied Flycatcher	T
Empidonax hammondii	Mosquero de Hammond	Hammond's Flycatcher	WR
Empidonax wrightii	Mosquero gris	Gray Flycatcher	WR
Empidonax occidentalis	Mosquero barranqueño	Cordilleran Flycatcher	PR
Empidonax sp.	Mosquero	Flycatcher	*
Tyrannus vociferans	Tirano gritón	Cassin's Kingbird	PR
Vireo solitarius	Vireo anteojillo	Blue-headed Vireo	WR
Vireo huttoni	Vireo reyezuelo	Hutton's Vireo	PR
Aphelocoma ultramarina	Chara pecho gris	Mexican Jay	PR
Corvus corax	Cuervo común	Common Raven	PR
Stelgidopteryx serripennis	Golondrina ala serrada	Northern Rough-winged Swallow	PR
Poecile sclateri	Carbonero mexicano	Mexican Chickadee	PR
Baelophus wollweberi	Carbonero embridado	Bridled Titmouse	PR
Psaltriparus minimus	Sastrecillo	Bushtit	PR

Table 1. Cont.

Species	Common Name (Spanish)	Common Name (English)	Residency
Sitta carolinensis	Sita pecho blanco	White-breasted Nuthatch	PR
Sitta pygmaea	Sita enana	Pygmy Nuthatch	PR
Certhia americana	Trepador americano	Brown Creeper	PR
Thryomanes bewickii	Chivirín cola oscura	Bewick's Wren	PR
Troglodytes aedon	Chivirín saltapared	House Wren	WR
Regulus calendula	Reyezuelo de rojo	Ruby-crowned Kinglet	WR
Polioptila caerulea	Perlita azulgris	Blue-gray Gnatcatcher	PR
Polioptila melanura	Perlita del desierto	Black-tailed Gnatcatcher	PR
Sialia sialis	Azulejo garganta canela	Eastern Bluebird	WR
Myadestes occidentalis	Clarín jilguero	Brown-backed Solitaire	PR
Catharus guttatus	Zorzal cola rufa	Hermit Thrush	WR
Turdus migratorius	Mirlo Primavera	American Robin	PR
Toxostoma curvirostre	Cuitlacoche pico curvo	Curve-billed Thrasher	PR
Melanotis caerulescens	Mulato azul	Blue Mockingbird	V
Bombycilla cedrorum	Ampelis chinito	Cedar Waxwing	WR
Ptilogonys cinereus	Capulinero gris	Gray Silky-flycatcher	PR
Phainopepla nitens	Capulinero negro	Phainopepla	PR
Peucedramus taeniatus	Ocotero enmascarado	Olive Warbler	PR
Vermivora celata	Chipe corona naranja	Orange-crowned Warbler	WR
Vermivora crissalis	Chipe crisal	Colima Warbler	SR
Parula superciliosa	Parula ceja blanca	Crescent-chested Warbler	PR
Dendroica coronata	Chipe Coronado	Yellow-rumped Warbler	WR
Dendroica townsendi	Chipe negroamarillo	Towsend's Warbler	WR
Dendroica occidentalis	Chipe cabeza amarilla	Hermit Warbler	WR
Dendroica sp.	Chipe	Warbler	*
Mniotilta varia	Chipe trepador	Black-and-white Warbler	WR
Wilsonia pusilla	Chipe corona negra	Wilson's Warbler	WR
Myioborus pictus	Chipe ala blanca	Painted Redstart	PR
Piranga flava	Tángara encinera	Hepatic Tanager	PR
Piranga sp.	Tángara	Tanager	PR
Pipilo maculatus	Toquí pinto	Spotted Towhee	PR
Pipilo fuscus	Toquí pardo	Canyon Towhee	PR
Aimophila cassinii	Zacatonero de Cassin	Cassin's Sparrow	PR
Spizella passerina	Gorrión ceja blanca	Chipping Sparrow	PR
Spizella pallida	Gorrión pálido	Clay-colored Sparrow	WR
Melospiza lincolnii	Gorrión de Lincoln	Lincoln's Sparrow	WR
Melospiza sp.	Gorrión	Sparrow	*
Junco phaenotus	Junco ojo de lumbre	Yellow-eyed Junco	PR
Pheucticus melanocephalus	Picogordo tigrillo	Black-headed Grosbeak	PR

Table 1. Cont.

Species	Common Name (Spanish)	Common Name (English)	Residency
Passerina caerulea	Picogordo azul	Blue Grosbeak	PR
Passerina cyanea	Colorín azul	Indigo Bunting	WR
Icterus wagleri	Bolsero de Wagler	Black-vented Oriole	PR
Icterus graduacauda	Bolsero cabeza negra	Audubon's Oriole	PR
Icterus parisorum	Bolsero tunero	Scott's Oriole	PR
Euphonia elegantisima	Eufonia capucha azul	Elegant Euphonia	PR
Carduelis psaltria	Jilguero dominico	Lesser Goldfinch	PR

Ralph (1996) with a fixed radius of 20 m for 10 minutes. Birds captured with mist nets were banded and released. Species were recorded following the systematic nomenclature of the A. O. U. (1998; 2000; Banks et al. 2002; Banks et al. 2003). Their permanency status was determined on the basis of field observations and information provided by Howell & Webb (1995). Guilds were considered following Ehrlich et al. (1988). Shannon's Diversity Index (1948) and Sorenson's Index of Similarity (1948) were used to obtain diversity and similarity indices.

RESULTS AND DISCUSSION

Based on records obtained by systematic sampling (point counts or mist nets), 1,080 individuals corresponding to 83 species, 62 genera, 31 families and 9 orders were recorded (Table 1). Seventy percent (54 species) of the species were defined as permanent residents, followed in number by winter residents with 22% (17 species), summer residents with 4% (3 species), transients with 3% (2 species), and vagrants with 1% (1 species).

The Oak Forest contained the highest number of species and individuals (58 and 473, respectively), followed by Pine-Oak Forest (48 and 360, respectively), and finally Pine Forest (40 and 251, respectively). The avian community appears distributed into discrete guilds (Table 2) with insectivorous species (42 species, 73%) being the major group in Oak Forest. It is suggested that this is determined by the availability of food (primarly insects) in the Oak Forests, resulting from generally more humid conditions than that of other forest types and the capacity of *Quercus* bark to support a major richness and abundance of invertebrates.

Table 2. Number of avian species for guilds and type of vegetation.

Guilds	Total		Pine Forest		Pine-Oak Forest		Oak Forest	
	# Sp.	%	# Sp.	%	# Sp.	%	# Sp.	%
Carrion	2	2.4	1	2.5	1	2.1	2	3.4
Prey	4	4.8	3	7.5	2	4.2	1	1.7
Insectivorous	62	75	30	75	36	75	42	72.8
Granivorous	4	4.8	2	5	3	6.2	4	6.8
Nectivorous	4	4.8	2	5	4	8.3	3	5.1
Omnivorous	3	3.4	1	2.5	2	4.2	2	3.4
Frugivorous	4	4.8	1	2.5	0	0	4	6.8

Table 3. Similarity Matrix for vegetational communities (Sorenson's Index).

	Pine Forest	Pine-Oak Forest	Oak Forest
Pine Forest		0.465	0.403
Pine-Oak Forest			0.485

Although Shannon diversity values were very similar across vegetation types, the highest was the Oak Forest (H' = 3.16), followed by Pine Forest (H' = 2.84), and lowest for Pine-Oak Forest (H' = 2.75). Evenness values were similar across all vegetation types; ranging in value from 0.71 (Pine-Oak Forest) to 0.78 (Oak Forest) to 0.77 (Pine Forest). The Pine-Oak Forest showed the lowest evenness values as a consequence of lower homogeneity in the avian community compared to the other vegetational associations.

The least similar avian communities based on Sorenson's Index were Oak Forest and Pine Forest (Table 3), which shared only 40% of the same species. By contrast, each of these was more similar to Pine-Oak Forest, sharing 48.5% and 46.5% of the species, respectively.

The seasonal distribution of species diversity is shown in Figure 1. The high value for Spring appears to be due to the presence of late winter and early summer migratory species in addition to permanent residents. In Fall, there are occurrences of late summer and early

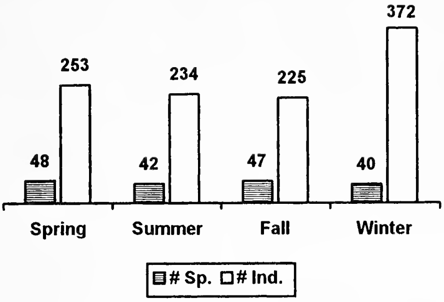

Figure 1. Seasonal distribution of avian richness and abundance. Numbers indicate the number of species and individuals captured during the study period.

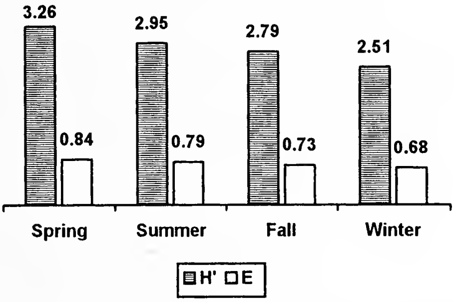

Figure 2. Shannon's Index (H') and evenness (E) values for each season.

Table 4. Similarity Matrix for seasons (Sorenson's Index).

	Spring	Summer	Fall	Winter
Spring		0.489	0.510	0.464
Summer			0.331	0.281
Fall				0.472

winter migrants that result in a greater number of species during this season. Both Spring and Fall appear to be transitional seasons where the replacement of bird species takes place. It is suspected that the high abundance of birds during Winter is due to winter residents and transients that migrate in numerically large groups, providing a lower homogeneity in the avian community during this season (Figure 2). The highest similarities among seasons were Spring and Fall (51%) and the lowest when comparing Summer and Winter (28.1%) (Table 4).

CONCLUSIONS

The most diverse avian communities were observed in Oak Forests and during the Spring. However, although noticeable differences in richness and abundance of birds exist among the vegetational communities and seasons compared, values for diversity and evenness are very similar. This leads the authors to conclude that avian communities in Pine, Pine-Oak, and Oak Forests in the Sierra San Antonio-Peña Nevada system are stable and homogenous throughout the year.

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MATE GUARDING IN NORTHERN MOCKINGBIRDS (*MIMUS POLYGLOTTOS*)

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Abstract.—The northern mockingbird, *Mimus polyglottos*, is a socially monogamous passerine. Behavioral observations during the fertile (nest building and egg laying) and the non-fertile (incubation) stages were used to determine the presence of paternity assurance behaviors. Mockingbird pairs remained close (within 5 m) 76.3% of the time during the fertile period. Median intrapair distance changed significantly from 4.8 m during the fertile period to 11.3 m during the non-fertile period. Males followed females significantly more during the fertile stage than the non-fertile stage. In addition, males sang the most during the fertile period. The male perched higher than the female in all of the breeding stages. Male northern mockingbird behavior was consistent with the mate guarding hypothesis. However, an alternative hypothesis, i.e., that males remain close to females to ensure copulation at the fertile stage, could not be rejected.

Ninety percent of bird species are considered monogamous (Lack 1968), however many of these species engage in copulations outside the pair bond (termed extra-pair copulations or EPCs). Extra-pair fertilizations (EPFs) result when EPCs are successful. Studies employing modern molecular techniques show that EPFs are common in many bird species with some populations containing 70% extra-pair young (Griffith et al. 2002). In some species females pursue EPCs, which suggests that they benefit from EPC behavior (Kempenares et al. 1992; Neudorf et al. 1997; Double & Cockburn 2000). Potential benefits of EPFs to females include better quality genes for the offspring (Fujioka & Yamagishi 1981; Kempenaers et al. 1992; Burley et al. 1994; Hasselquist et al. 1996), increased genetic variability of the offspring (Birkhead 1993; Petrie et al. 1998) or material benefits such as being allowed to feed on the territory of extra-pair males (Gray 1997). In addition, the extra-pair males may direct aggression toward predators on the territories of their extra-pair females (Gray 1997).

In many bird species, mate guarding is a common paternity assurance behavior (reviewed in Birkhead & Møller 1992). Mate guarding is defined as any behavior that functions to reduce the likelihood of encounters between a female and other males during the time when the female is fertile (Hatch 1987). A common form of mate guarding is closely following a mate during her fertile period (Beecher & Beecher 1979; Birkhead et al. 1987; Ritchison et al. 1994). Such behavior may influence a females' behavior, for example, in pied flycatchers (*Ficedula* *hypoleucia*), the risk of EPCs increases as the distance between pair members increases (Alatalo et al. 1987). Evidence suggests that an intrapair distance greater than 10 m significantly increases the number of EPCs and EPC attempts (Alatalo et al. 1987).

Northern mockingbirds (*Mimus polyglottos*) are socially monogamous but bigamy does occur occasionally (e.g. Laskey 1941). Low EPF frequencies (6.9% of broods, 3.1% of offspring) have been reported for a Texas population of mockingbirds (DeLoach 1997). The low level of EPFs may indicate mockingbirds do not regularly pursue EPCs and thus male paternity guards would not be necessary (Birkhead & Møller 1992). Alternatively, male mate guarding may be effective in preventing females from obtaining extra-pair matings (e.g. Chuang-Dobbs et al. 2001, but see Stutchbury and Neudorf 1998). The purpose of this study was to determine if male northern mockingbirds use mate guarding as a paternity assurance strategy. If mate guarding exists, it was predicted that males would maintain a closer proximity to females, a higher perching position than females, and would follow females more during the fertile period than in the non-fertile period.

METHODS

Species and study area.—This study was conducted on the campus of Sam Houston State University (SHSU) in Huntsville, Walker County, Texas, during April-August 2000 and 2001. SHSU is a 85-ha residential campus with an abundance of trees and manicured lawn. Hedge rows, shrubs and trees were common nesting sites of northern mockingbirds on campus.

Mockingbirds were trapped using walk-in Potter traps baited with mealworms. Each individual was banded with a U.S. Fish and Wildlife aluminum band and a unique combination of three plastic color bands for visual identification. Sex of individual mockingbirds was determined using behavioral cues (e.g., song) and the presence of a brood patch or cloacal protuberance.

Nests were located by following females and males and by checking likely nest sites such as dense shrubs and low dense trees (Joern & Jackson 1983; Means & Goertz 1983). For this study, the female's fertile period was defined as the period from the initiation of nest building to the laying of the penultimate egg (Birkhead & Møller 1992), which was typically 7-10 days.

Behavioral observations.—Over two breeding seasons, 12 different breeding pairs were observed during either the fertile (n = 6 pairs, 11

h) or nonfertile (n = 6 pairs, 9 h) stages. Ideally, the same female would have been watched during both the fertile and nonfertile stage, however, predation and nest desertion were common on the study site making observations throughout the nesting cycle difficult. No pairs were feeding fledglings from a previous brood at the time of observations but some of the nests were the second or third nesting attempt for the season. To determine if and to what extent mate guarding took place, the behavior of individual pairs was sampled during two, 1-h observation periods during the females' fertile (nest building and egg laying) or nonfertile (incubation) period. Watches were conducted only on pairs whose nest had been located and thus their nest stage was known at the time of the watches. Incubation watches included time females spent on and off the nest. Nest predation and inclement weather prevented two observations from being completed on 4 pairs. Thus, 1 pair at the fertile stage and 3 pairs at the nonfertile stage were watched for 1 h only. Mate guarding behaviors quantified included: (1) Intra-pair distance – distance (m) between a paired male and female every 2 min; (2) Height above mate – recorded which sex was perched higher (m) every 2 min; (3) Movement initiation – determined the frequency that 1 pair member followed the other within 15 sec of a pair member initiating a movement. A movement was defined as flying or walking in a directed manner for at least 1 m from the original position; (4) Song – recorded at 2 min intervals if the male was singing; (5) Fights – noted any observations of fights or intrusions into the focal territory by neighboring individuals or intrusions onto a neighboring territory by focal individuals. Fights were defined as aggression between two individuals that involved contact. Perch height and intra-pair distances were estimated visually by the observer. All observations were conducted by RYB.

Statistical Analyses.—Nonparametric statistics were used due to non-normal data and small sample sizes. Behavior at fertile and non-fertile stages was compared with Mann-Whitney U tests. Wilcoxon signed-rank tests were used to compare male and female behavior. All tests are one-tailed unless indicated otherwise. StatView, V. 5 (SAS Institute, Inc., Cary, NC) was used for all analyses.

RESULTS

Males remained closer to their mates during the fertile period than during the non-fertile period (Table 1). Males were also within 5 m of the female significantly more during the female's fertile period (Mann Whitney U test, $U = 0.0$, $P = 0.002$), with males within 5 m of

Table 1. Median (lower, upper interquartile range values) of mate guarding behaviors of northern mockingbirds during the fertile and nonfertile stages.

Variable [a]	Fertile $n=6$	Nonfertile $n=6$	U [b]	p
Intra-pair distance (m)	4.8 (3.7, 5.3)	11.3 (9.7, 15.5)	0.0	0.002
Time male is < 5 m	23.3 (20.0, 26.0)	10.5 (2.0, 12.0)	0.0	0.002
Male follows female	2.8 (1.0, 3.0)	0.5 (0, 2.0)	7.0	0.038
Female follows male	1.5 (1.0, 2.0)	0.3 (0, 1.0)	7.0	0.072 [c]
Male perched above female	14.8 (13.5, 15.5)	15.5 (13.5, 21.0)	14.5	0.285
Female perched above male	3.8 (3.0, 4.0)	5.5 (3.5, 9.0)	11.0	0.26 [c]
Neither perched higher	12.3 (10.5, 13.0)	8.5 (5.0, 12.5)	10.5	0.228
Male song	17.5 (14.5, 18.0)	10.0 (4.0-13.0)	6.5	0.032
Male fighting	0.0 (0, 1.0)	.75 (0, 1.0)	14.5	0.271

[a] Time within 5m, perching and male song are measured as number of 2-min intervals the individuals engaged in behavior. Following and fighting are reported as actual number of times the behaviors occurred.

[b] Fertile and non-fertile stages were compared with a Mann-Whitney test: U values and P values are adjusted for ties.

[c] Indicates two-tailed tests.

females 76.3% of the time during the fertile period and 25.8% of the time during the non-fertile period.

Males also followed mates more during the fertile period than the non-fertile periods (U = 7.0, $P = 0.038$, Table 1). Females exhibited a similar tendency, but differences were not significant. During the fertile period, females initiated 64.2% of the pair movements and males initiated 35.8%, and this difference approached significance (Wilcoxon signed-rank test, z = -1.9, $P = 0.058$, two-tailed).

During the fertile period, males more often perched higher than females perched higher (z = -2.2, $P = 0.014$). However, the number of 2-min intervals during which males were perched higher than females was not significantly different between the fertile and non-fertile periods (U = 14.5, $P = 0.29$, Table 1). In 40.9% of the time intervals during the fertile stage and 27.1% of the non-fertile time intervals, neither pair member was perched higher than the other and this behavior did not differ between nest stages (Table 1).

The average percent time males spent singing was 57% during the fertile period, which declined to 33% during incubation. There was a significant difference in song frequency between the fertile and non-fertile stages (U = 6.5, *P* = 0.032). There was no difference in male fighting behaviors between breeding stages (Table 1). No copulations or copula-tion attempts were observed during observation periods.

DISCUSSION

These findings support the mate guarding hypothesis. Male northern mockingbirds spent more time within 5 m of mates when they were fertile than when they were non-fertile. This behavior may function to prevent other males from approaching and pursuing EPCs with their mates (Birkhead & Møller 1992). Males also followed females more during the fertile period (Table 1) and this may act to maintain proximity (e.g., Beecher & Beecher 1979; Dickinson & Leonard 1996).

Male mockingbirds perched higher than females during both the fertile and non-fertile periods. Therefore, this behavior is probably not specific to mate guarding. A higher perching position may permit males to more easily defend their territories, observe neighboring females for extra-pair mating opportunities and be vigilant for predators (Carlson et al. 1985). Hobson and Sealy (1989) found that male yellow warblers (*Dedroica petechia*) perched higher than females throughout the nesting cycle and they also suggested multiple benefits to this behavior in addition to a possible mate guarding function.

Song output by male mockingbirds was more frequent during the fertile period, which agrees with previous mockingbird studies (Logan 1983). Møller (1991) reported that males may use song in a mate guarding context, however this does not appear to be the case in mockingbirds. Logan (1988) found playbacks of song during the fertile period did not elicit more aggressive responses in male mockingbirds than did playbacks at incubation. If song functioned in mate guarding then males would be expected to respond to playbacks more aggressively while their mates were fertile.

Studies of the effectiveness of mate guarding have generated equivocal results (e.g. Alatalo et al. 1987; Møller 1987; Kempenaers et al. 1995). Despite intense mate guarding relatively high EPFs still occur in many passerine species (e.g. Kempenaers et al. 1995; Wagner et al. 1996). The fact that mockingbirds have such low EPFs may indicate they do not regularly pursue EPFs or that males are extremely effective in preventing EPFs. The frequency of EPFs in one population of northern mockingbirds is relatively low (6.9% of 130 broods contained extra-pair young, Deloach 1997) compared to many other passerines (see Griffith et al. 2002). Although EPFs can vary between populations of the same species (Bjørnstad & Lifjeld 1997), there is no reason to expect this population would have a significantly different EPF frequency than that reported by Deloach (1997). The population is located in a similar habitat (urban college campus) and is located only 120 km north of Deloach's population.

Alternative hypotheses may explain male proximity to the female at the fertile stage (Birkhead & Møller 1992; Dickinson & Leonard 1996). The "copulation access hypothesis" states that males remain close to females more often at the fertile stage to increase within-pair copulation opportunities. This hypothesis predicts males should remain close to females during the times when copulations are more likely to occur (Birkhead and Møller 1992). In many species, copulations occur most frequently in the morning (e.g. Birkehead et al. 1987) whereas in others there is no diurnal pattern (e.g. Vernier et al. 1993; Hanski 1994). To the author's knowledge, the timing of within-pair copulations in mockingbirds has not been studied. To test the copulation access hypothesis, observation trials would be needed at different times throughout the day. Presumably males should remain closer to their mates in the morning (or the time of day that copulations normally occur) if it increases their opportunities for copulation. Conversely, males maintaining proximity for mate guarding purposes should be vigilant throughout the day as extra-pair copulations can potentially occur at any time of day (Venier et al. 1993).

The "predation hypothesis" states that males maintain proximity to females to act as sentinels and warn females when predators are near. This hypothesis predicts that both males and females should equally attempt to remain in close proximity to facilitate male vigilance (Dickinson & Leonard 1996). However, it was found that male mockingbirds were more likely to follow females than the reverse, which supports the mate guarding hypothesis.

In conclusion, male northern mockingbirds exhibited behaviors consistent with paternity assurance strategies. Males remained closer and followed their mates more frequently at the fertile stage. These behaviors have typically been regarded as methods to prevent females from engaging in EPCs. However, one cannot completely rule out alternative explanations for the observed behaviors. Future studies should focus on potential extra-pair mating tactics in mockingbirds to determine the extent to which mate guarding behavior may be selected for in males.

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TEXAS J. SCI. 56(3):215-222 AUGUST, 2004

A LATE CRETACEOUS DUROPHAGUS SHARK, *PTYCHODUS MARTINI* WILLISTON, FROM TEXAS

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Abstract.—The Late Cretaceous durophagus shark previously described as *Ptychodus connellyi* (Family Ptychodontidae) by MacLeod & Slaughter is here diagnosed as a junior synonym of *Ptychodus martini* Williston. The occurrence of the holotype (SMU-SMP 69031) in the Roxton Limestone Member (upper Lower Campanian) of the Gober Chalk in Fannin County, Texas is significant both geographically and stratigraphically. Whereas the present fossil record suggests that *P. martini* is endemic to the Western Interior Sea, this specimen represents the only record of *P. martini* outside Kansas. If the tooth was not subjected to any significant reworking, the specimen not only represents the youngest occurrence for the species, but also one of the youngest occurrences of the genus and family.

Ptychodus is a Cretaceous shark genus occurring in Albian to Early Campanian marine deposits of North and South America, Europe, Africa and Asia (Cappetta 1987). The genus is known primarily by its teeth, which are characterized by a massive crown suited for crushing shelled macroinvertebrates (durophagy: e.g., see Kauffman 1978; Stewart 1988a). Based on articulated specimens (e.g., MacLeod 1982), teeth were arranged in parallel rows in both the upper and lower jaws, forming a pavement-like dentition.

Species of *Ptychodus* are differentiated on the basis of variations in dental morphology (e.g., Cappetta 1987). The tooth crown of *Ptychodus* is generally square to rectangular when viewed occlusally, and the central portion of the crown surface has several parallel or radial ridges. Surrounding the central portion of the crown is the marginal area, which exhibits various textural patterns (e.g., granular, concentric, radial) formed by numerous small ridges, pits and tubercles. The crown rests on top of a massive tooth root, which may be weakly bilobed. The tooth root is smaller in dimension than the crown and has many foramina located at the crown-root interface. The criteria used to distinguish various species of *Ptychodus* include crown height, the configuration and number of ridges on the tooth crown, and the ornamentation on the marginal area.

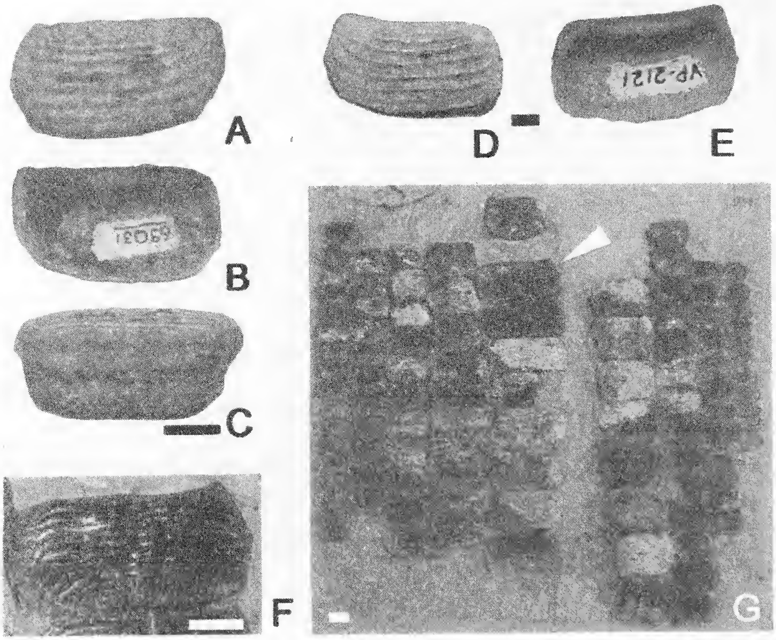

Figure 1. *Ptychodus martini* Williston 1900a: (A) Occlusal view of SMP-SMU 69031 from Roxton Limestone Member (upper Lower Campanian) of Gober Chalk, Texas, initially described as *P. connellyi* MacLeod & Slaughter 1980; (B) basal view of SMP-SMU 69031; (C) anterior view of SMP-SMU 69031; (D) occlusal view of FHSM VP-2121 from Smoky Hill Chalk Member of Niobrara Chalk, Kansas; (E) basal view of FHSM VP-2121; (F) occlusal view of one of the teeth in holotype of *P. martini* (KUVP 55277: see Fig. 1G) from Smoky Hill Chalk Member of Niobrara Chalk, Kansas, which resembles SMP-SMU 69031 and FHSM VP-2121; (G) entire view of holotype of *P. martini* (KUVP 55277: arrow points to tooth shown in Fig. 1F). Scale bar = 5 mm.

MacLeod & Slaughter (1980) described a new species of *Ptychodus*, *P. connellyi*, based on a single tooth (Figs. 1a-c) recovered from the Roxton Limestone Member (Lower Campanian) of the Upper Cretaceous Gober Chalk (Fig. 2) in northeastern Texas. This specimen (the holotype) remains the only known example of the species (Welton & Farish 1993, p. 58). However, comparisons with other *Ptychodus* specimens suggest that *P. connellyi* is conspecific with another species, *P. martini* (Williston 1900a). Therefore, the purpose of this paper is to reinterpret the holotype as *P. martini*, and discuss the geographic and stratigraphic significance of the specimen. Specimens in the following institutions are discussed in this paper: Fort Hays State University, Sternberg Museum of Natural History (FHSM), Hays, Kansas; the University of Kansas Vertebrate Paleontology Collection (KUVP), Lawrence, Kansas and the Shuler Museum of Paleontology at Southern Methodist University (SMP-SMU), Dallas, Texas.

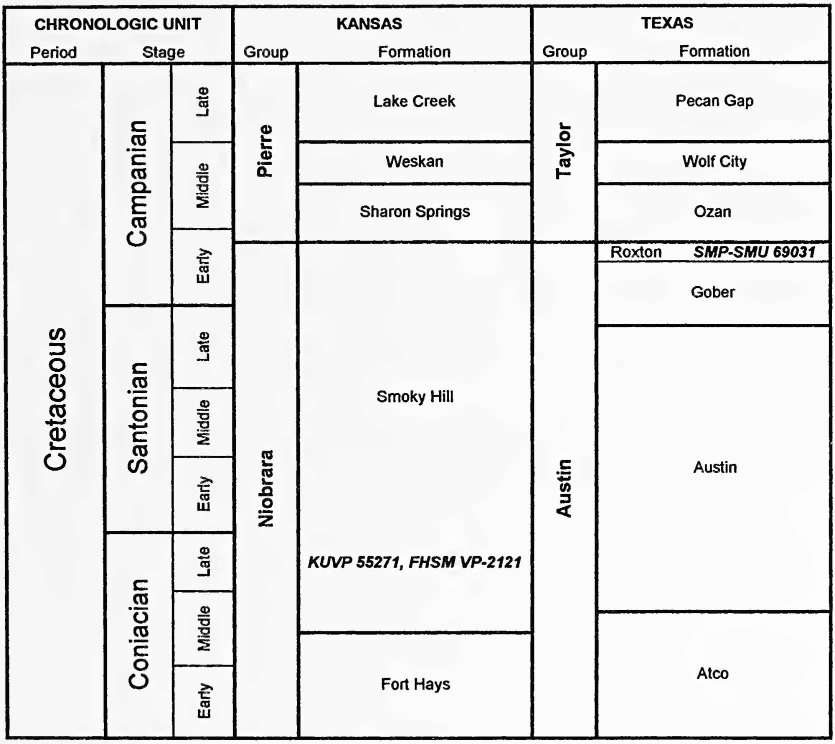

Figure 2. Generalized Upper Cretaceous stratigraphy (formations and members) of western Kansas and northeastern Texas (after Kennedy et al. 1997), indicating the stratigraphic horizons of *Ptychodus martini* specimens.

SYSTEMATIC PALEONTOLOGY

Ptychodus martini Williston 1900a

Material.—SMP-SMU 69031 (Figs. 1a-c), a single tooth initially described as *Ptychodus connellyi* MacLeod & Slaughter (1980).

Occurrence.—Roxton Limestone Member of the Gober Chalk (Fig. 2) exposed along the banks of Brushy Creek, 1.5 miles (2.4 km) southeast of the town of Barkley Woods, Fannin County, Texas (MacLeod & Slaughter 1980: Fig. 3).

Description.—SMP-SMU 69031 is rectangular when viewed occulusally and measures 37 mm wide and 21 mm in anteroposterior length. The crown is flat and measures only 5 mm in height. Eight low transverse ridges extend over much of the surface, and the marginal area

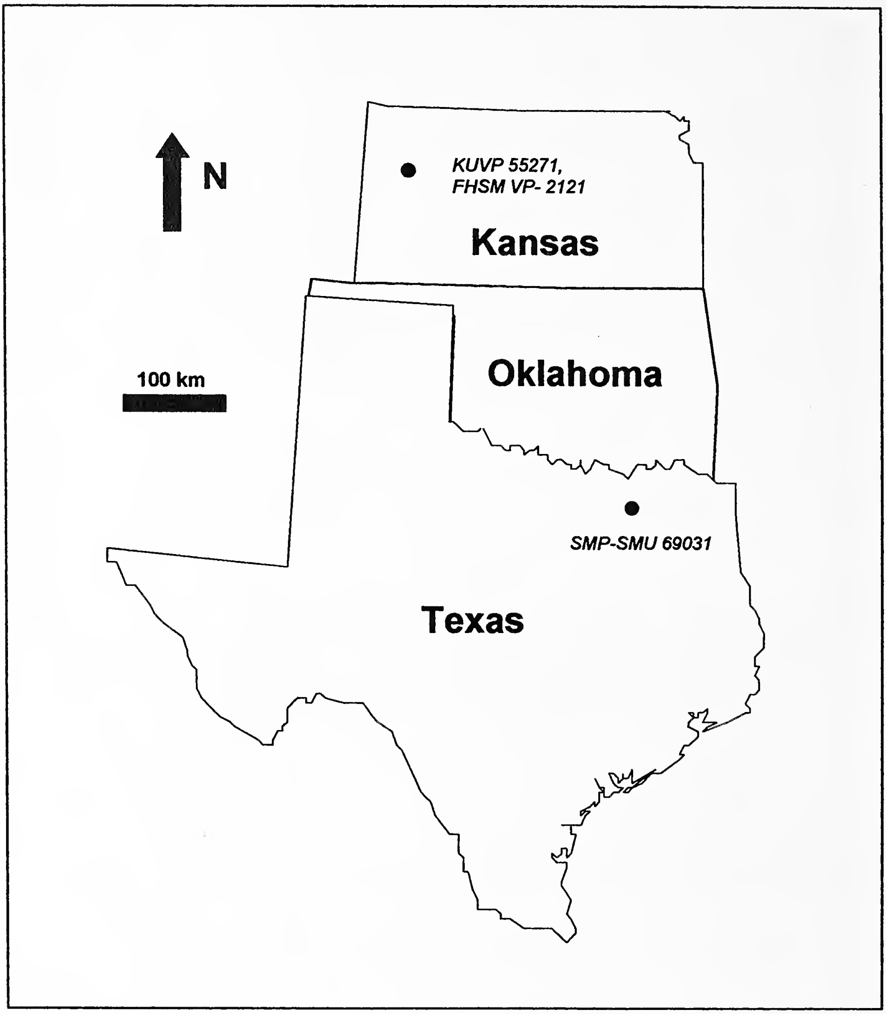

Figure 3. Geographic distribution of *Ptychodus martini* teeth recovered.

is very narrow and smooth lacking any ornamentation. However, this lack of ornamentation appears to be due to weathering as the tooth exhibits signs of abrasion. The tooth root is tabular and porous, and lacks a nutrient groove. The total tooth height (crown + root) is 16 mm.

DISCUSSION

Taxonomic remarks.—Based on SMP-SMU 69031, MacLeod & Slaughter (1980) differentiated *Ptychodus connellyi* from all other *Ptychodus* species by the flat occlusal surface (i.e., without an elevated cusp). However, observations suggest that the morphology of SMP-SMU 69031 (Fig. 1a-c) closely resembles teeth from the median row in the holotype of *P. martini* (KUVP 55277: Figs. 1f-g) and FHSM-2121 (Figs. 1d-e) recovered from the Upper Cretaceous Smoky Hill Chalk Member of the Niobrara Chalk in western Kansas. Because of their close resemblance, and the fact that no other *Ptychodus* species possess rectangular teeth with a flat occlusal surface (e.g., see Cappetta 1987; Welton & Farish 1993), the authors consider *P. connellyi* to be conspecific with *P. martini*. Because *P. martini* Williston (1900a) was described earlier than *P. connellyi* MacLeod & Slaughter (1980), *P. connellyi* is considered a junior synonym of *P. martini* following the International Code of Zoological Nomenclature (ICZN 1999).

Anatomical remarks.—The holotype of *Ptychodus martini* (Fig. 1g) consists of a set of 110 teeth. Although they were discovered disassociated, the teeth presumably come from an individual shark and were arranged artificially (for naturally arranged, general dental pattern of *Ptychodus*, see Woodward 1911). The occlusal surfaces of some teeth in the specimen are exceptionally flat and possess low, thin transverse ridges that extend fully to the marginal area. These are interpreted to come from the median tooth row because they are the largest, most symmetrical teeth in the dentition. Other teeth in the dentition, which are interpreted to represent teeth of lateral rows, are less elongate and have a slightly elevated crown with wider marginal areas. The morphology of SMP-SMU 69031 (Figs. 1a-c) suggests that the tooth is from the medial tooth row (cf. Fig. 1f).

Geographic remarks.—Reports on *Ptychodus martini* are scarce. The only previously reported specimens are KUVP 55277 (holotype: Williston 1900a; 1900b; Schultze et al. 1982, p. 13; Fig. 1g) and FHSM VP-2121 (isolated tooth: Hamm 2002; Figs. 1d-e) from western Kansas. The occurrence of *P. martini* in Texas is significant because it extends the geographic distribution of the species from the Western Interior to near the Gulf of Mexico (Fig. 3). Nevertheless, the present fossil record suggests that *P. martini* is endemic to the Western Interior Sea.

Stratigraphic remarks.—The genus *Ptychodus* had a nearly worldwide distribution from Albian to Campanian time (Cappetta 1987; Welton & Farish 1993). The two previously reported *P. martini* specimens (KUVP 55277 and FHSM VP-2121) occurred in the Smoky Hill Chalk Member of the Niobrara Chalk (Fig. 2). Stewart (1990, p. 24) noted that *P. martini* occurs only in his *Protosphyraena pernicosa* biozone (Stewart 1988b). This biozone corresponds to Hattin's (1982) lithostratigraphic Marker Units 1, 2 and 3, which are collectively Late Coniacian in age.

In northeastern Texas, the Gober Chalk is interpreted to be the upper tongue of the Austin Chalk (Stephenson 1927). The uppermost part (0.3-3 m) of the Gober Chalk, referred to as the Roxton Limestone (Fig. 2), consists of skeletal limestone rich in inoceramid [*Inoceramus balticus* (Boehm)] and ammonite remains (Fisher 1965). The occurrence of the ammonites *Menabites delawarensis* (Morton) and *Scaphites hippocrepis* (deKay) dates the Roxton Limestone as late Early Campanian in age (Cobban & Kennedy, 1992).

The surface of the *Ptychodus martini* tooth described in this paper (SMP-SMU 69031) shows extensive signs of abrasion (Figs. 1a-c). The abrasion could have resulted from a combination of pre-burial depositional activities and/or reworking. Because it was recovered from the banks of Brushy Creek (Macleod & Slaughter 1980), the abrasion may also be due to modern fluvial processes. It should be noted that the only Upper Cretaceous rocks in which Brushy Creek cuts through are the Gober Chalk (including the Roxton Limestone) and the overlying Ozan Formation (Fig. 2) where it intersects with the main channel of the North Sulphur River (based on UTBEG 1966; Mark McKenzie pers. comm. 2002).

Ptychodus has been reported from the Albian to the Campanian in North America (e.g., Williston 1900a; Applegate 1970; Meyer 1974; Cappetta 1987). Dibley (1911) reported 17 teeth of *P. polygyrus* Agassiz from northern France in the zone of *Actinocamax quadratus* (De Blaiville), which is Early Campanian in age. Schwimmer & Williams (1994) reported the occurrence of *P. mortoni* in an early Early Campanian deposit in eastern Alabama. If indeed SMP-SMU 69031 occurred in the Roxton Limestone (with no or insignificant reworking), the specimen is important because it represents the youngest occurrence of *P. martini* (giving the stratigraphic range of the taxon from Late Coniacian to late Early Campanian). Together with Dibley (1911) and Schwimmer & William's (1994) data, the specimen also marks one of the youngest occurrences for the genus *Ptychodus* and family Ptychodontidae (see also Cappetta et al. 1993).

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TEXAS J. SCI. 56(3):223-230 AUGUST, 2004

NEW RECORDS OF THE TEXAS HORNSHELL *POPENAIAS POPEII* (BIVALVIA: UNIONIDAE) FROM TEXAS AND NORTHERN MEXICO

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Abstract.—The Texas hornshell (*Popenaias popeii*) is reported and documented from the South Concho River in west central Texas and the Río Sabinas of northern Coahuila, both new site records. These records confirm the known distributional range of this species in the Colorado River drainage of central Texas and establishes a new interior state record for Coahuila. Recently collected shell material of *P. popeii* is also reported from the Devils River above Amistad Reservoir and from the Río Salado above Falcon Reservoir.

Resumen.—El bivalvo texano conocido como concha cuerno (*Popenaias popeii*) es registrado en el Río Concho Sur en el centro-oeste de Texas y el Río Sabinas en el norte de Coahuila. Ambos sitios son nuevos registros geográficos. Estos registros confirman el ámbito de distribución conocido de la especie en el drenaje del Río Colorado del centro de Texas y establece un nuevo registro estatal interior para Coahuila. Especimenes de *P. popeii* tambien son registrados en el Río Devils arriba de la Presa La Amistad y en el Río Salado arriba de la Presa Falcón.

The freshwater bivalve *Popenaias popeii* was originally described from the "Devil's River and Río Salado, Texas" by Lea (1857) as *Unio popeii*. Both the designation of the type-locality as well as the scientific name have undergone subsequent revision. While the designation of the Devils River as one of the original collection sites of *P. popeii* by Lea (1857) is undisputed by subsequent authors, some confusion existed early relative to the exact location of the Río Salado. Lea (1857) originally placed it in "Texas". Stearns (1891) gave the location as "near Leon, Mexico" and noted additional specimens from the "Río Salado, New Mexico"; Singley (1893) referred to its location as "New Mexico" and Simpson (1914) cited its location as "New Leon, Mexico" (state of Nuevo León). Johnson (1999:21) noted that the lectotype USNM 85895 from the Río Salado in Nuevo León was "inadvertently" selected by Johnson (1974:115) as the "figured holotype."

The Texas hornshell historically ranged south in the coastal systems of northeastern México to at least the Río Cazones of Vera Cruz

(Johnson 1999). In addition to the Devils River and Río Salado, it has been found upstream in the Pecos River to Ward County in Texas (Singley 1893) and several locations in New Mexico (Cockerell 1902; Metcalf 1982; Lang 2000); upstream in the Rio Grande to sites just downstream of Big Bend, Brewster County, Texas (Howells 1994) as well as several Mexican tributaries of the lower Rio Grande (Johnson 1999). A shell found in the Llano River in 1972 at Castell in Llano County (Ohio State University Museum collection OSUM 1976.365) was reported by Howells et al. (1997). Both Howells (2001a) and Smith et al. (2003) have recently mapped the distribution of *P. popeii* from the drainage systems of Texas, New Mexico and northern Mexico.

As a result of recent field collections, this report documents additional range extensions for *Popenaias popeii* from west-central Texas and northern Coahuila. Additionally, recent examinations of several previously known collection localities were conducted in both Texas and México. Voucher specimens are deposited with the holdings of the Illinois National History Survey (INHS), the Instituto Tecnológico de Ciudad Victoria (ITCV) and the Angelo State University Natural History Collections (ASNHC). The following listing is abbreviated and cites only those synonymies/citations deemed relevant to this study.

Popenaias popeii (Lea 1857)

Texas Hornshell

Unio popeii.—Lea 1857:102; Binney 1863:387; Cockerell 1902:69; Diaz de León 1912:136; Simpson 1914:700; Johnson 1974:115.

Unio popei.—Stearns 1891:104; Singley 1893:322.

Elliptio popei.—Ortmann 1912:271; Strecker 1931:17; Murray & Roy 1968:26.

Elliptio (*Popenaias*) *popei.*—Frierson 1927:38.

Nephronaias (*Popenaias*) *popeii.*—Haas 1969:201.

Popenaias popei.—Heard & Guckert 1970:339; Burch 1973:16; Neck 1984:11; Neck & Metcalf 1988:262; Howells et al. 1996:93; Johnson 1999:21.

Popenaias popeii.—Metcalf 1982:45; Howells 2001a:62; Smith et al. 2003:333.

NEW RECORDS

South Concho River.—A single left valve was collected in 1991 from among flotsam at the low water crossing of the South Concho River and U.S. Highway 277 within the city limits of Christoval, Texas. Heavy flooding had occurred in the area several weeks prior to the collection date.

Material examined.—South Concho River in Christoval (N 31°11'15" W 100°29'59"), Tom Green County, Texas, 21 July 1991, a single left valve (INHS 29012).

Remarks.—All previous records of *Popenaias popei* from Texas except the single specimen from the Llano River reported by Howells et al. (1997) have been made from the Rio Grande or its tributaries. This current record is noteworthy in that the South Concho River, like the Llano River, is a tributary of the Colorado River drainage system. The exact nature of the significance of these distributional records of *P. popeii* from the Colorado River drainage currently remains unknown. Numerous additional collections by Texas Parks and Wildlife Department from 1992 through the present failed to find any other specimens of *P. popeii* in the Llano or Concho rivers, or elsewhere in the Colorado drainage basin (Howells 2001b). Collected along with the single specimen of *P. popeii* were several single valves of *Cyrtonaias tampicoensis* (Tampico pearlymussel).

Río Sabinas.—Specimens of *Popenaias popeii* were initially collected from the dry river bed of the Río Sabinas in the Río Los Sabinitos Park area on Highway 20 (Coahuila) just west of Río Villa de San Juan Sabinas, Coahuila in August of 2001. A second collection in January of 2002 was made approximately 0.5 km upstream from the original site.

Material examined.—Río Sabinas west of Río Villa de San Juan Sabinas (N 27°55'23" W 101°18'21"), Coahuila, Mexico, 2 August 2001, three complete sets of valves (INHS 29013); 19 January 2002, three complete sets of valves (ITCV 8002), three complete sets of valves (ASNHC 0049).

Remarks.—Although this report represents the first interior record (other than the Rio Grande) of nonfossil material of *Popenaias popeii* from the state of Coahuila in northern Mexico, it should be noted that the Río Sabinas is an upstream tributary of the Río Salado. At the time of the collections in August 2001 and January 2002, the Río Sabinas was completely dry and without any evidence of recent water flow. Workers in the municipality of Sabinas, approximately 20 km downstream from the collection site, reported a cessation of water flow in the Río Sabinas in the spring of 2000. Dead shell material of *Cyrtonaias tampicoensis* and *Utterbackia imbecillis* (paper pondshell) was also present in the dry river bed.

Additionally, the Río Sabinas was examined approximately 50 km downstream from the municipality of Sabinas at Juárez just before the river enters the impoundment of the Presa Don Martín (listed on some maps as Presa Venustiano Carranza). At this location (N 27°36'42" W 100°43'29"), the river is accessible beneath the Highway 35 (Coahuila) bridge. Metcalf (1982) earlier reported fossil material of *Popenaias popeii* from this location. On 27 October 2001 and 3 March 2002 the river exhibited no flow and was characterized by a series of large isolated pools. Numerous intact pairs of valves of dead specimens of *Cyrtonaias tampicoensis* and *Utterbackia imbecillis* were common along the bank and shallow soft substrate of the stream bed. No specimens of *Popenaias popeii* were found.

PREVIOUSLY REPORTED RECORDS

In addition to collection efforts in the South Concho River and the Río Sabinas, both of the originally designated type-localities of the Devils River and Río Salado as well as the Llano River were revisited in an effort to assess the current existence of specimens of *Popenaias popeii* at each of these three different locations.

Devils River.—Considerable anthropogenic changes have occurred in the area of the lower Devils River since the original collection of *Popenaias popeii* in the 1800's. The Amistad Reservoir Dam (Presa La Amistad) was completed on the Rio Grande between Texas and México in 1968. The resulting lake area included the confluence of the Rio Grande with both the Devils River and the Pecos River. *Popenaias popeii* requires a shallow stream environment and is not currently known from impoundments (Lang 2000); consequently the man-made Amistad Reservoir does not appear to provide suitable habitat for this species. The area of the Devils River immediately above the lake level was examined in July of 2001.

Material examined.—200 m upstream from the confluence of the Devils River and Amistad Reservoir (N 29°39'54" W 100°55'58"), Val Verde County, Texas, 14 July 2001, two complete (but damaged) sets of valves and broken shell material from two additional specimens (ASNHC 0050). All of the *P. popeii* shell material was old and weathered; no fresh shell material was found at this location.

Remarks.—Despite changes associated with the construction of the Amistad Reservoir Dam, that section of the Devils River immediately above the current lake level appears to provide a physical habitat capable of sustaining extant populations of *Popenaias popeii.* While the presence of the above recently collected shell material of *P. popeii* in July of 2001 would appear to support the above proposal, only additional and more detailed field studies in this area can determine the current status of this species in the lower Devils River. Collected along with the specimens of *P. popeii* in 2001 were valves of *Cyrtonaias tampicoensis*.

Río Salado.—In a fashion similar to that of the Devils River, the Río Salado has also undergone considerable anthropogenic changes since the original collection of *Popenaias popeii* in the 1800's. Falcon Dam (Presa Falcón) was constructed on the Rio Grande between Texas and Mexico in 1953. The resulting Falcon Reservoir included the confluence of the Río Salado with the Rio Grande. As previously mentioned in reference to Amistad Reservoir, the resulting reservoir does not appear to provide suitable habitat for adult specimens of *P. popeii*. The area of the Río Salado above the lake level was examined in March of 2002.

Material examined.—Río Salado 100 m downstream from bridge on Highway 2 (Mexico) in northern Tamaulipas (N 26°47'23" W 99°25' 20"), 2 March 2002, a single heavily worn right valve (ASNHC 0051).

Remarks.—At the time of the March 2002 collection, the Río Salado exhibited no flowing water in the area of the Highway 2 bridge. The river was characterized by a series of large pools, which were separated by narrow bars of exposed substrate. Numerous intact pairs of valves of dead specimens of *Cyrtonaias tampicoensis*, *Utterbackia imbecillis* and *Quadrula apiculata* (Southern mapleleaf) were common in the stream bed.

Anáhuac.—Río Salado beneath and downstream of the Highway 1 (Nuevo Leon) bridge within the municipality of Anáhuac, Nuevo Leon (N 27°14'1.4" W 100°08'21.9"), 2 June 2002; three complete sets of valves and four single valves (one of the single valves was very recent) (ASHC 0052).

Remarks.—The river at the time of the collection exhibited no detectable flow and was under considerable influence of untreated household waste pollutants. Several specimens of *Cyrtonaias tampicoensis* and *Utterbackia imbecillis* were also found at this location.

Llano River.—A single specimen of *Popenaias popeii* collected in

1972 was reported by Howells et al. (1997) from the Llano River (N 30°42'13" W 98°57'32") and the crossing of Highway 2768 at Castell in Llano County. Several recent visits in 1992, 1997, 1999, 2000 and 2001 to the Castell area yielded no additional specimens of *P. popeii*.

Corbicula sp.

Shell material of the Asian clam was present at every collection site in both Texas and México examined during the course of this study and is therefore not individually reported as part of the additional faunal listings.

DISCUSSION

This study extends the known range of *Popenaias popeii* to include the South Concho River of west central Texas and the Río Sabinas of northern Coahuila. It also confirms the earlier report of this species by Howells et al. (1997) from the Colorado River drainage system of central Texas.

These additional extensions to the known range of this freshwater bivalve would initially appear to represent positive indications to the overall conservation status of this species. It should be noted, however, that current conditions related to reduced water flow, drying of stream beds, or both, in the Río Salado and Río Sabinas of northern México do not appear capable of supporting significant populations of *Popenaias popeii*. While isolated or protected areas of both of these rivers or their tributaries may in fact support limited numbers of surviving individuals or populations, the decline in suitable habitat in the area of northern Tamaulipas, Nuevo León and Coahuila does not appear favorable to the overall survivability of this species.

Even though heavy rains in April of 2004 returned the Río Sabinas to normal flow, the Devils, Llano and South Concho rivers of Texas currently appear to provide a greater range of both available and seemingly suitable habitat for maintaining *Popenaias popeii* than do most of the rivers of northern México. However, no extant populations are currently known from these three rivers. These rivers appear to provide both adequate levels of water and the necessary current flow capable of maintaining surviving populations of *P. popeii*. Very little is known about this species in Texas and no living specimens were observed during the course of this study. The extreme rarity of recovered shell material from both the Llano and South Concho would appear indicative of populations at or near the extinction level in these two rivers. Indeed, the only known populations of *P. popeii* are present in a short stretch of the

Black River, New Mexico (Lang 2000; Howells 2001a) and the Rio Grande, Webb County, Texas (Howells 2003, 2004), with recently dead shells found in the Rio Grande between Big Bend and the mouth of the Pecos River, Texas, suggesting survivors may also persist there as well (Howells 2004). Additional and more detailed study would be required to determine the current status of this species in the rivers of west central Texas. However, this study indicates that *P. popeii* is at least rare or endangered throughout its range in Texas and New Mexico.

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PARABOLOIDS FOR MAXIMUM SOLAR ENERGY COLLECTION

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Abstract.—Paraboloids of revolution have been used for many purposes such as searchlights, radars and other operations concentrating on the broadcasting of waves. This article is a study of some variations of these ideas.

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1. *Parabolas*.-Let $F(0,p)$ by the focus of $y = -p$ the directrix of the parabola $x^2 = 4py$ (Fig. 1). It is well-known that the tangent line PT to the parabola at any point P is the bisector of the angle between PF and PH, the perpendicular from P to the directrix. This implies that the normal of P, PN, is the bisector of the corresponding supplement angle (Fig. 2). This idea suggests that some parabolic surfaces are useful in collecting solar energy. A few samples will be given.

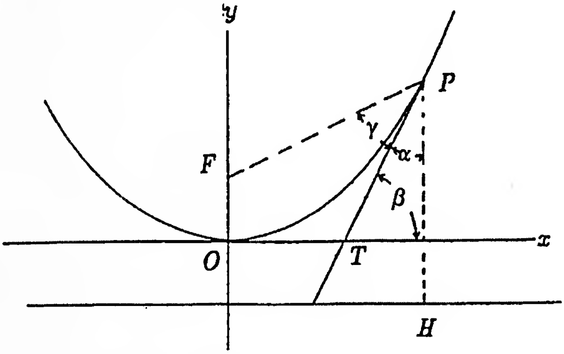

Fig. 1

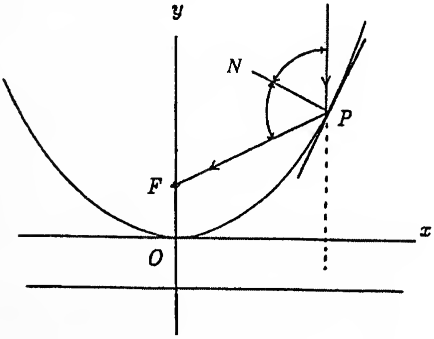

Fig. 2

2. *Paraboloid of revolution.*–Rotating a parabola about its axis, one obtains a paraboloid of revolution (Fig. 3). Since any plane containing the axis of rotation intersects the paraboloid in a parabola of the same size as the original one, the paraboloid has a single focus *F*. Thus *F* collects the maximum amount of energy when the rays are parallel to the axis. Indeed, this is quite well known and will not be further elaborated here.

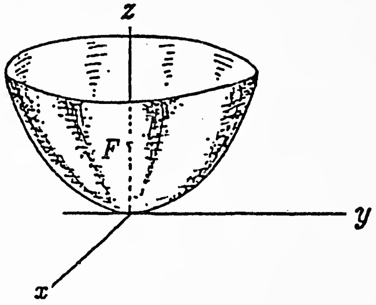

Fig. 3

3. *Elliptic Paraboloids.*–Consider a concave mirror of elliptic paraboloid shape. The equation of the corresponding surface can be chosen to be

$$z=\frac{x^2}{a^2}+\frac{y^2}{b^2}$$

where *a* and *b* are positive real numbers and we may choose $a > b$ (Fig. 4). Consider a plane containing the *z-axis*. This plane intersects the *xy*-plane in a line. Choose an axis *Ot* on this line. Let

$$(l,m)=(\cos a,\sin a),\ 0\leq a<\pi$$

be the set of direction cosines of *Ot*. It is clear that this will give all possibilities of the intersection of the *tz*-plane with the paraboloid,

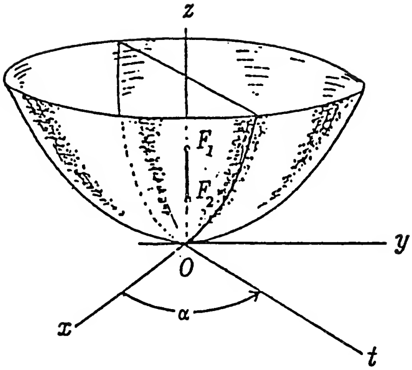

Fig. 4

as follows:

$$\left[\begin{array}{l} x=lt \\ y=mt \\ z=\frac{x^2}{a^2}+\frac{y^2}{b^2}, l^2+m^2=1 \end{array}\right. \tag{1}$$

One obtains

$$z=\frac{b^2l^2+a^2m^2}{a^2b^2}t^2 \tag{2}$$

which is a parabola in *tz*-plane (Fig. 4).

Note that $(l,m) = (1,0)$ corresponds to $z = \frac{x^2}{a^2}$ and $(l,m) = (0,1)$ corresponds to $z = \frac{y^2}{b^2}$.

In general the focus of the parabola is at

$$(0,0,\frac{a^2b^2}{4(b^2l^2+a^2m^2)})$$

In particular one observes that

$$F_1=(0,0,\frac{a^2}{4}) \textit{ also } F_2=(0,0,\frac{b^2}{4})$$

are respectively the foci of

$$z=\frac{x^2}{a^2} \text{ also } z=\frac{y^2}{b^2}.$$

Note that

$$\frac{b^2}{4} < \frac{a^2b^2}{4(b^2l^2+a^2m^2)} < \frac{a^2}{4} \tag{3}$$

Indeed (3) shows that the line segment F_1F_2 extracts the maximum energy.

4. *Parabolic tubes*.—Consider a parabolic cylinder (Fig. 5). Let the equation of this cylinder be

$$z=ax^2,\ a>0.$$

One can easily see that there is a line of foci whose equations are

$$x=0,\ z=\frac{1}{4a}.$$

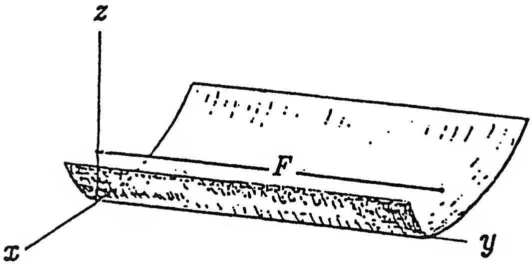

Fig 5

Indeed a concave mirror of this shape is able to collect enough energy that one can cook a shish kabob or roast hot dogs in the line of the foci.

A parabolic cylinder is the simplest parabolic tube. One may study other tubes which collect more energy. Two interesting ones shall be studied.

Consider the parabola

$$y=\frac{1}{2b}(x^2-b^2).$$

Rotating this parabola about the *x-axis*, one obtains

$$y^2+z^2=\frac{(x^2-b^2)^2}{4b^2}.$$

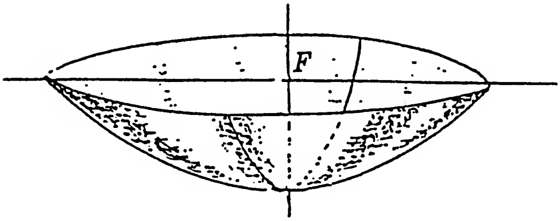

Fig. 6

It is clear that every plane that contains the *x-axis* intersects this surface in a parabola whose focus is the origin (Fig. 6). Thus a portion of this surface may be used as a concave mirror for collecting energy.

Now rotating the parabola about a line perpendicular to its axis which does not pass through the focus, one obtains another tube. Consider the parabola

$$y=a(x^2-b^2), a\neq\frac{1}{2b}, a > 0, b > 0.$$

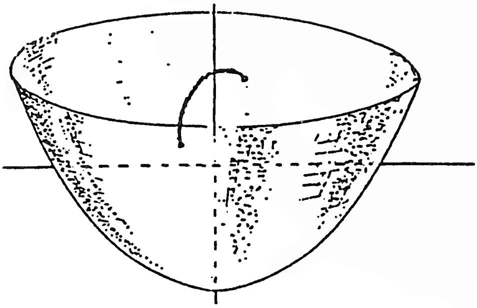

Fig. 7

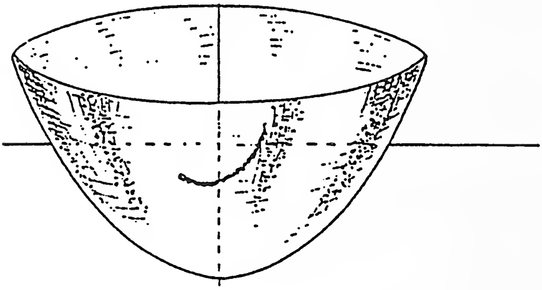

Fig. 8

Let the focus be at (0,q). Now we rotate the parabola about the x-axis. A portion of this surface may be made into a concave mirror. If $q > 0$, then we obtain a circular locus of foci which arches downward (Fig. 7), while if $q < 0$, one obtains a circular arc of foci bending upwards (Fig. 8). In this latter case one can collect the maximum amount of energy from rays along this concave arc.

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CHARACTERISTICS OF PERIPHERAL POPULATIONS OF PARTHENOGENETIC *CNEMIDOPHORUS LAREDOENSIS* A (SQUAMATA: TEIIDAE), IN SOUTHERN TEXAS

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Abstract.—From 1984-2004 the distributional ecology of the parthenogenetic *Cnemidophorus laredoensis* (= *Aspidoscelis laredoensis*) complex both north and south of the Rio Grande between Amistad Reservoir and the Gulf of Mexico was studied. Although dozens of sites inhabited by clonal complex A of *C. laredoensis* were discovered within a few km of the river (over a geographic range in parts of Webb, Zapata, Starr and Hidalgo counties, Texas, and Tamaulipas State, México), the species was observed at only three sites in two Texas counties that were widely removed and apparently disjunct from the river-centered zone. In order to better understand what factors limit the distribution of *C. laredoensis* A, these three most distant sites from the Rio Grande (55.5 to 75.5 km) where this hybrid-derived species is in syntopy with maternal progenitor *C. gularis* (= *Aspidoscelis gularis*): Catarina, Dimmit County, and Encinal and Artesia Wells, La Salle County, Texas were studied. Each peripheral site was characterized by sandy substrate that is known to be one of the most important requirements for *C. laredoensis* A. The relative amounts of the original thorn scrub vegetation favorable to *C. gularis* and chronically disturbed habitat favorable to *C. laredoensis* A at each site constituted the major determinant of the relative size of populations of the two species. The absence of *C. laredoensis* A north of these sites in Dimmit and La Salle counties is probably a result of ecological resistance to expansion consisting of unsuitable substrate and vegetation. There was no evidence that a low frequency of hybridization between normally parthenogenetic females of *C. laredoensis* A and males of *C. gularis* or periodic collection of *C. laredoensis* A at Catarina and Artesia Wells measurably destabilized these populations.

The hypothesis that diploid parthenogenetic *Cnemidophorus laredoensis* (McKinney et al. [1973]; = *Aspidoscelis laredoensis* sensu Reeder et al. [2002]; Sauria: Teiidae), represents the descendants of one hybrid female between the gonochoristic species *C. gularis* and *C. sexlineatus* (= *Aspidoscelis gularis* and *A. sexlineata* respectively, sensu Reeder et al. [2002]) has received support from electrophoretic studies (McKinney et al. 1973; Parker et al. 1989; Dessauer & Cole 1989), mitochondrial DNA analysis (Wright et al. 1983), and skin histocompatibility experiments (Abuhteba 1990; Abuhteba et al. 2000; 2001). This mode of origin for clonal complex A of *C. laredoensis* necessitated an improba-

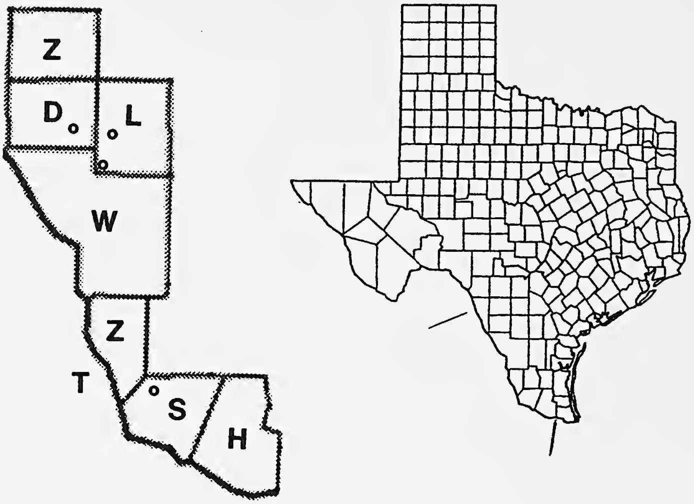

Figure 1. Map of Texas and position (line) of the counties (top Z = Zavala, D = Dimmit, L = La Salle, W = Webb, Z = Zapata, S = Starr and H = Hidalgo), Rio Grande, and state in México (T = Tamaulipas) referenced in this paper. *Cnemidophorus gularis* occurs in suitable habitats throughout the enlarged area, *C. laredoensis* A occurs in habitats in the immediate vicinity of the river in Webb, Zapata, Starr and Hidalgo counties and Tamaulipas and at outlying sites in Dimmit (open circle = Catarina), La Salle (upper circle = Artesia Wells and Lower circle = Encinal), and Starr (site marked by circle is not likely disjunct from the distribution of the species in the valley) counties, and *C. sexlineatus* is limited to parts of Dimmit, Webb (where marginal syntopy occurs with *C. laredoensis* A) and Starr counties.

ble sequence of events involving a single ancestral hybrid female: (1) its growth to adulthood in syntopy with both parental species; (2) initial avoidance of back crossing with *C. gularis* and *C. sexlineatus*; and (3) presence of cytogenetic determinants for production of eggs with parthenogenetic potential. Success of *C. laredoensis* A became possible when the descendants of the original hybrid completed fixation of parthenogenesis in successive generations and the incipient species "captured a habitat" (Wright & Lowe 1968).

The geographic range of *C. laredoensis* A is situated between the southern edge of the range of its paternal progenitor *C. sexlineatus* and the Rio Grande in parts of Webb (only known sites of syntopy are listed by Walker et al. 2001), Dimmit, La Salle, Zapata, Starr and Hidalgo counties, Texas, USA, and the riverine zone bordering México from Nuevo Laredo southeast to Nuevo Progreso, Tamaulipas, México (Fig. 1; see also Walker 1987a; 1987c; Walker et al. 1990; Paulissen & Walker 1998). Remarkably, unlike its largely allopatric relationship to *C. sexlineatus*, the entire range of *C. laredoensis* A has developed within a small part of the vast binational distributional area of its maternal progenitor *C. gularis* (Conant & Collins, 1998).

Despite extensive searching during over 50 expeditions from 1984-2004 involving both sides of the Rio Grande between Amistad Reservoir and the Gulf of Mexico, populations of *C. laredoensis* A have never been located more than about 80 km N or a few km S of the river (Walker 1987a; 1987c; Walker et al. 1990). In fact, all except three of the 51 sites discovered for this parthenogen were either located within 16 km N (n = 35) and 10 km S (n = 11) of the river or were apparently contiguous with this zone (n = 2 sites in Starr County). The other three are the most distant sites from the Rio Grande known for *C. laredoensis* A at 55.5 to 75.5 km to the north in Catarina, Dimmit County, and Encinal and Artesia Wells, La Salle County, Texas (Fig. 1). Several collecting trips were made to these peripheral sites inhabited by *C. laredoensis* A between 1986 and 2000 allowing (1) description of the habitat and substrate characteristics that affect whiptail lizards at each site; (2) estimation of the relative abundance of the parthenogen and *C. gularis* and characterization of the nature of syntopy between these species; (3) gauging of the impact of interspecific hybridization on both species at Artesia Wells and Catarina; and (4) estimation of the impact of collecting on populations of both species at each site. In this paper, the data obtained on these trips are used to identify the factors which may limit the distribution of *C. laredoensis* A in areas removed from the Rio Grande.

MATERIALS AND METHODS

The capture of a single individual of *C. laredoensis* A in September 1985 at Encinal, La Salle County, approximately 56 km from the Rio Grande, was the first indication that the species inhabited areas well removed from the river. Subsequently, JMW led a number of sanctioned collecting trips to explore surrounding areas of La Salle, Dimmit and southern Zavala counties in search of the parthenogen (Walker 1987a). Sites at Catarina, Valley Wells, Asherton, Carrizo Springs and 3.2 km southwest of Carrizo Springs in Dimmit County, sites at Artesia Wells, Cotulla, Gardendale and Millet in La Salle County, and two sites at Crystal City in southern Zavala County were explored (Walker 1987a; 1987c). Each site was systematically searched by three or more collectors and an attempt was made to collect all lizards seen with air guns; on average, about one in three lizards observed was captured. Collections were made between 0900 and 1700 CDT on clear to partly cloudy days in spring and summer during the peak period of whiptail lizard activity; visits were also made to some sites in September and October (Table 1).

Table 1. Acquisition dates and composition of collections/observations of *Cnemidophorus* from sites in Dimmit (Catarina, Valley Wells, and 3.2 km SW Carrizo Springs), La Salle (Encinal, Artesia Wells and Gardendale), and Zavala (Crystal City) counties, Texas (*C. laredoensis* = LAR, *C. gularis* = GUL, *C. sexlineatus* = SEX, *C. laredoensis x C. gularis* = HYB). Site Codes follow Walker (1987a).

SITES/DATES	LAR	GUL	SEX	HYB	SPECIMENS COLLECTED/OBSERVED
CATARINA (D-3)					
26 April 1986	7	0	0	0	LAR, UADZ 1431-1437
24 May 1986	14	10	0	3	LAR, UADZ 1642-1655; GUL, UADZ 1819-1828; HYB, UADZ 1944-1946
8 October 1987	3	0	0	0	LAR, UADZ 2731-2733 + 28 observed; GUL, 1 observed
13 May 1988	23	3	0	2	LAR, UADZ 2959-2974, 2976, 2981, 2982-2985 (= AMNH 146714-146717), 2986; GUL, UADZ 2978-2980; HYB, UADZ 2975, 2987
14 May 1988	2	0	0	0	LAR, UADZ 3022, 3023 (= AMNH 146718, 146719)
12 June 1988	3	0	0	0	LAR, UADZ 3118-3120
16 May 1989	4	1	0	1	LAR, UADZ 3502-3505; GUL, 3507; HYB, UADZ 3506
19 May 1989	5	1	0	1	LAR, 3542-3544, 3546, 3547; GUL, UADZ 3545; HYB UADZ 3541
31 July 1989	2	1	0	0	LAR, UADZ 3706, 3707 + 21 observed; GUL, UADZ 3708 + 3 observed
28 May 1995	7	5	0	0	LAR, UADZ 5456, 5460-5462, 5464, 5466, 5467; GUL, UADZ 5457-5459, 5463, 5465
7 September 1996	10	3	0	0	LAR, UADZ 5749, 5750, 5752-5759; GUL, UADZ 5748, 5751, 5760
TOTALS	80	24	0	7	
ARTESIA WELLS (L-2)					
26 April 1986	3	5	0	1	LAR, UADZ 1438-1440; GUL, UADZ 1630-1634; HYB, UADZ 1626
2 May 1986	0	4	0	0	GUL, UADZ 1626-1629
16 July 1986	3	2	0	1	LAR, UADZ 1951-1953; GUL 1998, 1999; HYB, UADZ 2017
19 May 1989	0	2	0	0	GUL, UADZ 3548, 3549
7 September 1996	6	3	0	0	LAR, UADZ 5764-5769; GUL, UADZ 5761-5763
8 September 1996	5	2	0	0	LAR, UADZ 5771, 5772, 5774-5776; GUL, 5770, 5773
31 August 1997	4	0	0	0	LAR, UADZ 5982-5985
TOTALS	21	18	0	2	

ENCINAL (L-3)					
6 September 1985	0	0	0	0	GUL, 25 observed
8 September 1985	1	0	0	0	LAR, UADZ 1376
26 April 1986	3	6	0	0	LAR, UADZ 1441-1443; GUL, UADZ 1635-1640
TOTALS	4	6	0	0	
GARDENDALE (L-4)					
16 July 1986	0	4	0	0	GUL, UADZ 1994-1997
10 July 1987	0	2	0	0	GUL, UADZ 2439, 2440
TOTALS	0	6	0	0	
VALLEY WELLS (D-2)					
24 May 1988	0	13	0	0	GUL, UADZ 1806-1818
3.2 KM SW CARRIZO SPRINGS ON FM 2644 (D-4)					
13 May 1988	0	5	16	0	GUL, UADZ 2988-2992; SEX, UADZ 2997-3012
14 May 1988	0	1	8	0	GUL, UADZ 3013; SEX, UADZ 3014-3021
16 May 1989	0	3	1	0	GUL, UADZ 3499-3501; SEX, UADZ 3498
TOTALS	0	9	25	0	
CRYSTAL CITY (ZA-1, ZA-2)					
26 April 1986	0	9	0	0	GUL, UADZ 1580-1588

In addition to the Encinal site among those listed above, *C. laredoensis* A was discovered only at Catarina and Artesia Wells, where it was syntopic with maternal progenitor *C. gularis*. Searches for whiptail lizards between Encinal, Artesia Wells and Catarina (and between the other sites in Dimmit, La Salle and Zavala counties listed) produced only specimens of the ubiquitous lizard *C. gularis*, plus numerous *C. sexlineatus* at 3.2 km southwest of Carrizo Springs. The populations of *C. laredoensis* A at Catarina, Artesia Wells, and Encinal are not only disjunct from each other, they are also separated from the principal distribution area of the species in the Rio Grande Valley and one area in Starr County likely contiguous to the valley. Some of the specimens of *C. laredoensis* A and *C. gularis* from Catarina, Encinal and Artesia Wells reported in this paper were also used in previous studies (Walker 1987a; 1987c; Walker et al. 1989; Abuhteba 1990; 2000; 2001; Walker et al. 1991; Paulissen et al. 1992). Specimens referenced in Table 1 are deposited in the University of Arkansas Department of Zoology (UADZ) and American Museum of Natural History (AMNH) collections.

Relative abundances of *C. laredoensis* A versus *C. gularis* were determined by comparing the numbers of each species caught at each site. The possibility that hybridization between *C. laredoensis* A and *C. gularis* at Catarina and Artesia Wells might limit both species by "wastage of gametes" was evaluated by tracking the number of hybrids captured during each collecting trip and comparing it to the relative numbers of the parental forms subsequently captured for evidence of a decline in their numbers. Finally, the impact of repeated collections on the population of *C. laredoensis* A at each site was gauged by totaling the number of lizards captured during each collecting trip and checking for a trend in declining numbers.

The habitat and substrate characteristics of each site were described following the methods of Walker (1987a; see also Walker 1987c; Paulissen et al. 2001). In brief, the relative amounts of undisturbed thorn scrub habitat (characterized by mesquite and/or huisache trees, scattered groundcover of a few bunchgrasses and prickly pear cactus, and a variety of small shrubs) and disturbed habitat (characterized by few trees and more abundant bunchgrass, low weeds, Russian thistle with numerous open patches, trails or roads running through) were estimated. The predominant substrate type (sand, loam or gravel) was also recorded. The nature of the habitat disturbance was also characterized as "catastrophic" if the site had been completely bulldozed and left

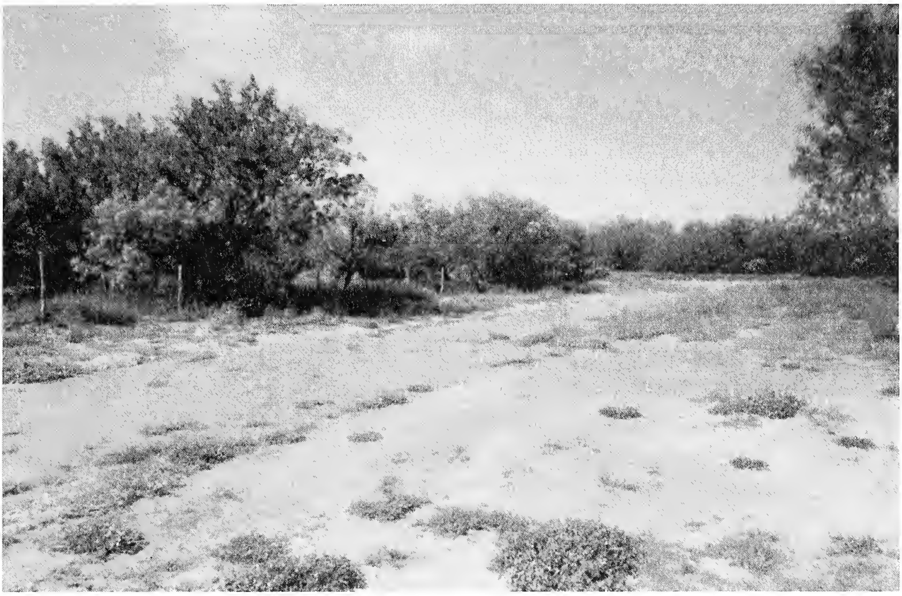

Figure 2. Photograph made in September 1996 showing part of the chronically disturbed site at Artesia Wells (L-2), La Salle County, Texas, inhabited by *Cnemidophorus laredoensis* A and *C. gularis* (note sparsely vegetated area in foreground with deep sandy soil, patch of mesquite on the left side of the road, and buffelgrass on the upper side of the road.

to recover on its own, as "chronic" if the site was intact but subjected to constant minor disturbance in the form of human or animal traffic, small scale agriculture or small scale clearing of brush (Fig. 2; Table 2).

RESULTS AND DISCUSSION

Characteristics of peripheral sites inhabited by Cnemidophorus laredoensis A.—In 11 visits to Catarina between 1986 and 1996 (Fig. 1), individuals of *C. laredoensis* A were located between sandy roadsides and mesquite-grass/weed associations (n = 8), in a vacant lot among grasses/weeds and scattered shrubs (n = 4) and in a trampled, overgrazed horse pasture (n = 68) (Table 1). The horse pasture is an approximately 4.25 acre rectangle (135 m by 137 m less a 21 m by 62 m part surrounding a house at the northwest corner) with intermittent thick growths of mesquite, scattered clumps of cacti, a weedy composite and deep sandy soil, characteristics that epitomized the type of habitat most successfully exploited by *C. laredoensis* A in the Rio Grande Valley (Table 2). As many whiptails as possible were collected from the horse pasture on each visit from 29 May 1986 through 9 September

1996 (*C. laredoensis* A, *n* = 68; *C. gularis*, *n* = 16; *C. laredoensis* A x *C. gularis* hybrids, *n* = 7). *Cnemidophorus laredoensis* A was both more generally distributed and numerically dominant compared with *C. gularis* in the chronically disturbed horse pasture throughout the study (Paulissen et al. [2001] listed the two species as equally abundant based on two visits in 2000; but this result was based on data taken on one trip when weather conditions were suboptimal for lizard activity). Although the possibility of finding individuals of *C. gularis* was enhanced by working in a border of mesquite trees along the north side of the horse pasture, occasional individuals of this species were also encountered elsewhere in the pasture. Areas outside of the pasture at Catarina were much less abundantly inhabited by *C. laredoensis* A and *C. gularis* (*n* = 8) and were apparently devoid of hybrids. The Catarina site was most recently visited by JEC on 4 June 2003 where the habitat previously described had remained intact.

At Artesia Wells (Fig. 1, 2), individuals of *C. laredoensis* A were collected and observed in the following open-structured grass/weed-mesquite associations: sandy roadsides (*n* = 6); in trampled, over-grazed cattle pens with cacti (*n* = 3); in the edge of cultivated areas (*n* = 2); and near human habitations (*n* = 10). The relatively low numbers of individuals of both *C. laredoensis* A and *C. gularis* collected/observed was due to the patchy/fragmented structure of the available habitat for whiptail lizards dispersed within an area of about six acres. The increased numbers of *C. laredoensis* A collected/observed at Artesia Wells in September 1996 compared with other visits (Table 1) resulted from a decision to collect within a few meters of human habitations which were avoided on previous occasions. *Cnemidophorus gularis* was mostly absent from such microhabitats and it was generally encountered in less disturbed areas of thorn scrub habitat near unpaved roads.

Encinal was the first site beyond the immediate vicinity of the Rio Grande where *C. laredoensis* was discovered (Fig. 1). The collection of a single specimen of this species (UADZ 1376) on 8 September 1985 at Encinal (in a weedy fence row north of Texas Hwy. 44 and east of a paved road paralleling railroad tracks) was a major breakthrough in understanding the distribution of the species north of the Rio Grande. Two days earlier (6 September 1985), JMW counted about 25 individuals of *C. gularis*, but did not observe *C. laredoensis* A, in a 5 m by 45 m strip of habitat with scattered shrubs and closely spaced bunchgrasses on the opposite side of the highway near the railroad. All other

Table 2. Habitat characteristics of the three peripheral sites north of the Rio Grande known to be inhabited by the allodiploid parthenogenetic species *Cnemidophorus laredoensis* A (*C. gularis* was present and *C. sexlineatus* was absent at all sites). Site Codes follow Walker (1987a).

CHARACTERISTIC	CATARINA (D-3)	ARTESIA WELLS (L-2)	ENCINAL (L-3)
1. Date of discovery of Population (visits)	26 April 1986 (11)	26 April 1986 (7)	8 September 1985 (3)
2. Location of site	Dimmit County, small settlement (>20 rural homes) E US Hwy 83	La Salle County, enclave (<10 homes) W I-35 at jct. FM 133	La Salle County, railyard W I-35 at jct. State Hwy 44
3. Distance from the Rio Grande	50.5 km	75.5 km	58.0 km
4. Nature of habitat	Chronically disturbed	Chronically disturbed	Catastrophically disturbed
5. Type of Disturbance	Grazing and trampling by horses, clearing by humans	Grazing and trampling by livestock, road grading, clearing by humans	Sand dumped along patches of weeds
6. Habitat components	Horse pasture, sandy roadsides, cleared vacant lots	Livestock pens, sandy roadsides, edge of fields, near houses	Open sandy flats bordered by weedy vegetation
7. Principal vegetation utilized by whiptails	Mesquite, cacti, weeds (pasture), bunchgrasses/weeds elsewhere	Mesquite, cactus, bunchgrasses, variety of weeds	Mesquite, bunchgrasses variety of weeds
8. Proportion of undisturbed thorn scrub at site	Less than half of the site	About half of the site	None at the site, abundant nearby
9. Predominant Soil	Sand	Sand	Sand (dumped from rail car)

individuals of *C. laredoensis* A collected or observed at Encinal were syntopic with *C. gularis* either immediately west of main street near a patch of sand spilled from railroad cars that had become interspersed with grasses/weeds on both sides of railroad tracks ($n = 2$) or in an adjacent weedy lot ($n = 1$ + several observed). The small number of *C. laredoensis* A observed at Encinal during the study were in patches of habitat within an area of about two acres (Table 2). The large number of *C. gularis* at parts of this site can be attributed to the initial migration of individuals from relatively undisturbed thorn scrub formations nearby into the altered grassy habitat in railroad-right-of-ways that typically are not preferred by *C. laredoensis* A.

Characteristics of peripheral sites not inhabited by C. laredoensis A.—Many unsuccessful searches for *C. laredoensis* A have been conducted in La Salle County north of Artesia Wells along I-35 (at Cotulla, Gardendale and Millett), in Dimmit County at sites other than Catarina (e.g., Valley Wells, Asherton, Carrizo Springs and SW of Carrizo Springs) and in parts of Zavala County (vicinity of Crystal City) (Fig. 1). The presence of *C. gularis* and absence of *C. laredoensis* at the Cotulla, Crystal City, Asherton and Carrizo Springs study sites is correlated with the habitat characteristics of gravelly (not sandy) substrate and relatively undisturbed thorn scrub vegetation. Gardendale, Millett, and 3.2 km SW of Carrizo Springs initially seemed suitable for habitation by *C. laredoensis* A based on the presence of deep sandy soil, although only the latter site closely duplicated the chronically disturbed vegetation structures found at Artesia Wells and Catarina. Only *C. gularis* was recorded on three visits to Gardendale and during two visits to Millett.

The site at 3.2 km SW of Carrizo Springs near FM 2644 inhabited by whiptail lizards comprised approximately five acres with sandy soil, large clumps of cacti, scattered mesquites and sparse ground cover of grasses/weeds that had been heavily trampled, trailed and grazed by cattle. Although this habitat type and pattern of chronic disturbance seemed ideal for *C. laredoensis* A, it was the parthenogen's paternal progenitor *Cnemidophorus sexlineatus* that was the most abundant whiptail lizard at the site ($n = 25$ + 10 observed); relatively few *C. gularis* ($n = 9$ + 5 observed) were present (Table 1).

The conclusion that neither *C. laredoensis* A nor *C. sexlineatus* were broadly distributed in La Salle and Dimmit counties was also supported by information pertaining to the 15, 200 acre Chaparral Wildlife Management Area provided by C. Ruthven (pers. comm.). This area is located 12.8 km west of Artesia Wells on Texas FM 133 in parts of both counties. Ruthven stated that since 1996 the Chaparral WMA staff had been sampling herpetofauna with drift fence arrays (totaling over 3900 drift fence days). They found that *Cnemidophorus gularis* is very common on the area (1,147 captures), *C. sexlineatus* is very rare (18 captures), but *C. laredoensis* A is absent.

Role of habitat and substrate characteristics in limiting C. laredoensis A.—The three sites in Dimmit and La Salle counties where *C. laredoensis* A has been found away from the Rio Grande are characterized by sandy soil and chronic to catastrophic habitat disturbance (e.g., Fig 2). Most of the other sites in these counties lacked either one of both of these critical habitat characteristics and so it is not surprising that *C. laredoensis* A did not occur at them. Further north, the substrate becomes generally less sandy; this combined with an more or less unbroken expanse of undisturbed thorn scrub habitat suggests that *C. laredoensis* A is unlikely to be found much further north than the Dimmit and La Salle county sites documented in this paper.

Potential role of interspecific hybridization with C. gularis.—Individuals of *C. laredoensis* A and *C. gularis* were occasionally observed in the same field of vision at Catarina and Artesia Wells and copulation between the two species was observed in the horse pasture at Catarina (Walker et al. 1991). That such copulations can lead to fertilization of the unreduced 2n = 46 eggs of normally parthenogenetic *C. laredoensis* A by the 1n = 23 sperm of *C. gularis* is indicated by the presence of hybrids of both sexes among the lizards obtained at Catarina and Artesia Wells.

The seven *C. laredoensis* x *C. gularis* hybrids from Catarina were identified as follows: five males based on morphological characters and erythrocyte nuclear diameters (UADZ 1944, snout vent length = SVL 65 mm; 1945, SVL 62 mm; 1946, SVL 66 mm; 2987, SVL 78 mm; 3506, SVL 62 mm); one subadult female based on erythrocyte nuclear diameters (UADZ 2975, SVL 55 mm); and one female based on skin histocompatibility experiments and triploid chromosome complement (UADZ 3541, SVL 74 mm). Confirmed hybrids constituted only 6.4% of all whiptails obtained at Catarina. The hybrid males were readily identifiable based on a dorsal pattern closely resembling *C. laredoensis*

A, ventral colors resembling *C. gularis*, low numbers of granules around midbody, and postantebrachial scales of intermediate size between the two parental species. That two females obtained at Catarina initially appeared to be individuals of *C. laredoensis* A based on color pattern, but were subsequently found to be hybrids based on other techniques, indicates that some female *C. laredoensis* A x *C. gularis* hybrids from this and other sites are not identifiable by external morphology. The most apparent meristic consequence of hybridization between the two species at Catarina was a reduction in the number of granules around midbody (mean 85.6, range 82-87, $n = 7$) in the confirmed hybrids.

Two *C. laredoensis* x *C. gularis* hybrids were collected at Artesia Wells, one male (UADZ 1626, SVL 69 mm) and one female (UADZ 2017, SVL 88 mm). The hybrid male was similar in color pattern to the five hybrid males from Catarina. The hybrid female resembled individuals of *C. laredoensis* A from Artesia Wells in dorsal pattern; however, it exceeded the maximum SVL of 80 mm for the species at the site and had a red-pink throat and remarkable purple-blue chest and abdomen resembling adult males of *C. gularis*. Erythrocyte nuclear diameters confirmed the hybrid status of both specimens.

Theoretically, fertilization of normally parthenogenetic females of *C. laredoensis* A by males of *C. gularis* could destabilize the parthenogen by reducing successful reproduction at sites such as Artesia Wells and Catarina (Cuellar 1977). To date, this outcome has not been documented for any pair of species of *Cnemidophorus*. At Catarina, seven hybrids were conclusively identified and an additional 10 specimens were putatively identified to *C. laredoensis* A (SVLs 44-71 mm) with such low numbers of granules around midbody (mean 85.8, range 83-88) as to arouse suspicion that they might also be hybrids (UADZ 1650 [24 May 1986]; 2733 [8 October 1987]; 2965, 2966, 2969, 2974, 2983, 2986 [13 May 1988]; 3544 [19 May 1989]; 3707 [31 July 1989]). Even if all these individuals are hybrids, the fact that so few have been collected over the span of four years, combined with the fact that the size of the *C. laredoensis* A population has shown no sign of declining (see below and Table 3), suggests that interspecific hybridization of *C. laredoensis* A with *C. gularis* is not an important factor affecting the population of the parthenogen at Catarina. Presumably the same is true at Artesia Wells.

Table 3. Summary of collecting success of each species and at the three peripheral sites inhabited by *Cnemidophorus laredoensis* A, *C. gularis* and hybrids in Dimmit and La Salle counties, Texas.

Site (Visits)	*C. laredoensis* A	*C. gularis*	Hybrids
Catarina (D-3, 11 visits)			
Captured/Observed	80/210 (38.0%)	24/44 (54.5%)	7/8 (87.5%)
Collected per visit	7.3	2.2	0.6
Artesia Wells (L-2, 6 visits)			
Captured/Observed	21/39 (53.8%)	18/22 (81.8%)	2/2 (100%)
Collected per visit	3.5	2.0	0.3
Encinal (L-3, 3 visits)			
Captured/observed	4/7 (57.1%)	6/40 (15.0%)	None
Collected per visit	1.3	2.0	—
Totals (20 visits)			
Captured/Observed	105/256 (41.0%)	48/104 (46.1%)	9/10 (90.0%)
Collected per visit	5.2	2.4	0.5

Impact of periodic collections.—Collecting trips to Catarina and Artesia Wells made over the span of several years allowed determination if removal of lizards had any effect on abundance of *C. laredoensis* A (or *C. gularis*). The fact that the number of lizards captured per trip does not show a decline from the first collecting trip to the last (Table 1) suggests that periodic collecting had no measurable impact on populations of either species. Negative impact of collecting on each population was mitigated by the infrequency of removal of individuals between 1985 and 1997 and escape behaviors of the species which reduced the effectiveness of all methods of collection. The yield (% of lizards observed that were collected per site) ranged from 38.0% at Catarina to 57.1% at Encinal for *C. laredoensis* A and from 15.0% at Encinal to 81.8% at Artesia Wells for *C. gularis* using air guns, large rubber bands and nooses (Table 3). Each of these methods was ineffective for collection of hatchlings of *C. laredoensis* A (Table 1, see 8 October 1987 and 31 July 1989 results). Overall, *C. laredoensis* A was the most abundant lizard at Catarina, *C. gularis* was the most abundant species at Encinal, and these two species were roughly equally abundant at Artesia Wells (Tables 1, 3).

Conclusions.—Cnemidophorus laredoensis A is one of the most abundant vertebrates at many sites within its restricted range in southern Texas and Tamaulipas. The ancestor of this parthenogenetic species originated at a site inhabited by *C. gularis* and *C. sexlineatus*, possibly either in northern Webb County, the only point of syntopy presently known for all three species, or in northern Starr County, where the ranges of *C. laredoensis* A and *C. sexlineatus* are separated by about 30 km and *C. gularis* occurs throughout the area. The 10-50 km wide separation of the ranges of *C. laredoensis* A from *C. sexlineatus* (extending from northern Webb County through Zapata, Starr and Hidalgo counties) is probably not a result of competitive exclusion of one species by the other. In the absence of major geographic barriers to the northward expansion of *C. laredoensis* A toward the range of *C. sexlineatus* and the southward expansion of *C. sexlineatus* toward the Rio Grande, it appears that both are hampered by subtle ecological barriers to expansion (i.e., substrate and/or vegetation structure). It is possible that *C. laredoensis* A has been able to expand more rapidly along both sides of the Rio Grande in a zone of frequent habitat disturbance (that may temporarily displace *C. gularis*) than northward from the river through more stable habitats (inhabited by *C. gularis*) toward the southern range limits of *C. sexlineatus*. Although both *C. laredoensis* A and *C. sexlineatus* are sand-loving species, the former is mostly limited to alluvial deposits (Walker 1987a) whereas the latter is mostly limited to broadly distributed eolian deposits where species of the lizard genus *Holbrookia* and the sandbur genus *Cenchrus* are ecological indicators (Paulissen et al. 1997). To rephrase the question posed by Paulissen et al. (1992) "Can parthenogenetic *Cnemidophorus laredoensis* (Teiidae) coexist with its bisexual (progenitors)?" the answer in the case of *C. sexlineatus*, broadly speaking, is no; the answer in the case of *C. gularis* is emphatically yes.

Broad syntopy between *C. laredoensis* A and maternal progenitor *C. gularis* within the range of the former in areas of Texas and México stems from one of two conditions. Syntopic contacts at sites such as Encinal, Artesia Wells and Catarina could involve a temporal dynamic in which one species is eventually excluded from the site by the interplay between interspecific competition and habitat characteristics. A stronger possibility is that syntopy is maintained through mitigation of these effects by a variety of responses (e.g., microhabitat selection, reproductive adaptations, tolerance of diet niche overlap and/or relaxed selection pressure in disturbed habitats: Paulissen et al. 1992; Paulissen 2001). That habitat structure and history of land use are crucial components in the complex syntopic relationship between *C. laredoensis* A and *C. gularis* at particular sites (Walker 1987a; 1987b; 1987c) is consistent with observations on these species at Encinal, Artesia Wells and Catarina. At each site, the amounts of relatively undisturbed thorn scrub vegetation favorable to *C. gularis* versus disturbed habitats favorable to *C. laredoensis* A constitute the major determinants in the relative size of populations of the two species (Tables 1, 2, 3). Catastrophic alteration of any of these sites would be expected to result in the reduction or exclusion of *C. gularis* and rapid repopulation by *C. laredoensis* A (Walker 1987b), whereas restoration of the original thorn scrub habitat would likely lead to the reverse of this outcome.

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COMPARISON OF BRANCH ELONGATION AMONG FOUR *ACACIA* SPECIES AND TEXAS EBONY IN THE LOWER RIO GRANDE VALLEY OF TEXAS

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Abstract.—Branch elongation was compared among four *Acacia* species (*Acacia berlandieri*, *A. farnesiana*, *A. rigidula*, *A. schaffneri*) and Texas ebony (*Chloroleucon ebano*) at three sites in Hidalgo and Starr counties, Texas. Most of the branch elongation occurred in fall and early winter in *A. berlandieri*, *A. farnesiana* and *A. rigidula*, but in *A. schaffneri* most of the growth occurred in late winter and spring. Branch elongation in Texas ebony was not concentrated in a given season. *Acacia berlandieri*, *A. farnesiana* and *A. rigidula* had significant positive correlations between branch elongation and rainfall, but *A. schaffneri* and Texas ebony did not. Variation in branch elongation among *Acacia* species is as great as that which occurs between the *Acacia* species and Texas ebony.

Phenological studies are important because they provide descriptive information essential to the elucidation of reproductive and growth patterns. Such studies are a crucial prelude to formulation of hypotheses in experimental investigations (Bullock & Solis-Magallanes 1990; Eddy & Judd 2003). There have been only two studies (Vora 1990; Eddy & Judd 2003) of the phenology of woody plants in the Lower Rio Grande Valley of Texas (LRGV). Vora (1990) reported on flowering, fruiting, leaf growth and leaf drop of 19 native species (most were woody) occurring primarily at Santa Ana National Wildlife Refuge, 12.1 km south of Alamo, Hidalgo County, Texas. He did not quantitatively analyze comparisons among species in the characteristics he examined, and he did not quantify the relationships between climatic factors and the reproductive and vegetative responses of the species studied. Eddy & Judd (2003) described and quantified the flowering and fruiting phenology of *Acacia berlandieri*, *A. minuata* (= *A. farnesiana*), *A. rigidula*, *A. schaffneri* and *Chloroleucon ebano* at two sites in Hidalgo County and one site in Starr County.

The objectives of this study were to: (1) describe and quantify patterns of branch elongation among four *Acacia* species (*A. berlandieri*, *A. farnesiana*, *A. rigidula* and *A. schaffneri*) and *Chloroleucon ebano*; (2) quantitatively examine the relationships between climatic factors and branch elongation of the species studied; and (3) determine if the magnitude of differences in branch elongation between members of the genus *Acacia* are as great as those between any of the *Acacia* species and *Chloroleucon ebano*. The null hypotheses tested were: (1) there are no significant differences in the patterns of branch elongation of the *Acacia* species studied; (2) variation in branch elongation among the *Acacia* species is less than the variation between any of the *Acacia* species and *Chloroleucon ebano*; and (3) there are no significant correlations between climatic factors and branch elongation.

MATERIALS AND METHODS

Study area.—The LRGV comprises the southernmost four counties of Texas (Cameron, Hidalgo, Starr and Willacy counties). This study was conducted in Hidalgo and Starr counties. The climate is semi-arid and subtropical. Summers are long and hot and winters are short and mild (Lonard et al. 1991; Eddy & Judd 2003). The mean length of the frost-free period is 330 days, but winters often pass without a freezing temperature. Mean monthly temperature is greater than 16°C in all months throughout the LRGV. In summer, a temperature of 32.5°C or greater occurs for 116 or more days.

Mean annual rainfall ranges from a high of 71.5 cm at Harlingen, Cameron County to a low of 54.9 cm at Rio Grande City, Starr County. From 28 to 33% of the annual rainfall occurs in September and October and 65 to 73% of the annual rainfall occurs from May through October. Most of the precipitation results from thunderstorms.

Vegetation of the study sites is brush grassland and thorn woodland (Lonard et al. 1991; Eddy & Judd 2003). Study sites were the Castilla Ranch (CR) 11.9 km north of Rio Grande City, Starr County, Yturria Brush Tract (YBT) 7.1 km west of La Joya, Hidalgo County and Santa Ana National Wildlife Refuge (SAN) 12.1 km south of Alamo, Hidalgo County.

Description of species.—*Acacia berlandieri* (guajillo) is a semi-evergreen shrub ranging in height from 1.0 to 4.0 m (Lonard et al. 1991; Everitt et al. 2002; Richardson 1995). It is found on a variety of soils, but is especially abundant in the LRGV on caliche soils in western Hidalgo and Starr counties. The leaves are fern-like, bipinnately compound, alternate and have 30 to 50 pairs of leaflets per pinna (Lonard et al. 1991; Eddy & Judd 2003). The flowers are white, and the legumes are 10.2 to 15.2 cm long with 5 to 10 dark brown seeds (Taylor et al. 1999; Eddy & Judd 2003).

Acacia farnesiana (huisache) is a small, spiny tree or shrub ranging from 2.0 to 4.0 m tall (Lonard et al. 1991; Everitt et al. 2002; Eddy & Judd 2003). It occurs on a variety of soil types (Lonard et al. 1991). The leaves are bipinnately compound, alternate, with 2 to 8 pairs of pinnae and 10 to 25 pairs of leaflets per pinna (Lonard et al. 1991). The flowers are yellow to gold, and the fruit can be reddish brown, purple, or black (Everitt et al. 2002). The legumes are 5.1 to 7.6 cm long and the seeds are in 2 rows within them (Everitt et al.2002; Taylor et al. 1999).

Acacia rigidula (black brush) is a white-spined, multiple-stemmed shrub that grows to a maximum height of 3.0 m (Lonard et al. 1991; Eddy & Judd 2003). It is often found with guajillo. Black brush is found on clay or gravelly soils in the LRGV (Richardson 1995). The leaves are alternate, bipinnately compound with 1 or 2 pairs of pinnae and 2 to 4 leaflets per pinna (Lonard et al. 1991). The flowers are yellowish or white. The legume is black to reddish black, 5.1 to 8.9 cm long, and constricted between the seeds (Richardson 1995; Taylor et al. 1999).

Acacia schaffneri (huisachillo) is a spiny, rounded shrub that grows to a maximum height of 2.0 m (Lonard et al. 1991). It occurs on sandy and clay soils in the LRGV (Richardson 1995). Leaves are alternate, bipinnately compound with 2 to 5 pairs of pinnae and 10 to 15 pairs of leaflets per pinna (Lonard et al. 1991). Flowers are yellow. The fruit is a linear, black, pubescent legume from 4.0 to 13.0 cm long and constricted between the seeds (Correll & Johnston 1979; Lonard et al. 1991; Everitt et al. 2002; Richardson 1995).

Chloroleucon ebano (Texas ebony) is a tree with a maximum height of 15 m (Richardson 1995), but usually it is less than 10 m tall (Lonard et al. 1991). It has zig-zag branches with stout stipular spines. The leaves are alternate or fascicled and bipinnately compound with 3 to 6 pairs of leaflets per pinna. Texas ebony occurs on sandy loam soils in the LRGV (Lonard et al. 1991). The flowers are white, and the fruit is a thick-walled woody legume.

Field and statistical methods.—Only black brush was present at all three study sites (Table 1). Each of the other four species was present at two sites. SAN and YBT each had four of the five species and CR had three species present. Ten individuals from each of the species

Table 1. Species present at study sites in Hidalgo and Starr counties. NWR = National Wildlife Refuge.

Species	Castilla Ranch	Santa Ana NWR	Yturria Brush Tract
Acacia berlandieri		X	X
Acacia farnesiana	X	X	
Acacia rigidula	X	X	X
Acacia schaffneri	X		X
Chloroleucon ebano		X	X

present at a site were marked for study. Shrubs (guajillo, huisachillo and black brush) were 1.5 m in height or taller. Huisache and Texas ebony were 3 m or taller. Shrubs and trees of these heights were known to be capable of possessing fruit. Distance between marked individuals ranged from 8 m to 2,320 m. All plants selected were healthy. Plants were marked with colored flagging and two aluminum tags bearing a unique identification number.

Branch elongation was monitored by applying a ring of paint just below the terminal bud on three randomly selected branches on each individual. The distance from the paint mark to the tip of the branch was measured to the nearest mm at monthly intervals from October 1998 through August 1999. The mean elongation of the three branches was recorded as the shoot elongation for the individual for a given month.

Daily air temperatures, precipitation and photoperiod were obtained from the National Climatic Data Center for McAllen, Texas. Long-term precipitation and temperature data were obtained from the Office of the Texas State Climatologist.

RESULTS

Mean monthly photoperiod at McAllen, Texas ranged from 10 h and 32 min in December 1998 to 13 h and 45 min in June 1999 (Table 2). The study sites varied from McAllen by less than 15 min latitude, so there was little variation between photoperiod at McAllen and any of the three study sites. Likewise, there was little variation in photoperiod among the study sites.

Because of the distance between the study sites and the distance between them and McAllen, it was possible that rain might have occurred at McAllen and not at any of the study sites. Likewise, it was

Table 2. Climatic data for McAllen, Texas.

Month	Rain (cm) 1998-99	Rain (cm) 1958-98	Mean Temp. (°C) 1998-99	Mean Temp. (°C) 1958-98	Mean Daylight (min) 1998-99
Sept.	24.09	11.11	28.7	29.1	738
Oct.	7.23	7.93	24.8	25.2	692
Nov.	2.61	2.82	21.6	20.6	652
Dec.	0.71	2.81	16.7	16.6	632
Jan.	0.08	3.74	18.2	15.0	643
Feb.	0.03	3.63	21.9	17.3	677
Mar.	5.74	2.02	23.0	21.1	721
Apr.	0.10	3.65	26.9	25.0	767
May	3.17	6.70	28.9	27.6	806
Jun.	1.27	7.06	30.9	29.9	825
Jul.	0.41	3.71	29.8	30.6	816
Aug.	7.82	5.51	31.2	30.9	782

possible that rain occurred at a study site and not at McAllen or that rain occurred at one study site and not at the other two sites. Using local observer reports it was previously shown (Eddy & Judd 2003) that there was less than 1.0 cm difference in monthly rainfall total of the SAN and YBT sites in all months of this study. The CR site generally was within 1.5 cm in monthly rainfall of the other two sites, but in October 1998, CR received 2.6 cm more rain than the other sites and in August 1999, CR received 3.0 cm less rain than the other two sites.

Branches were first marked for monitoring growth in length in October 1998. Consequently, November 1998 is the first month that data on branch elongation was reported. Rainfall in October and November 1998 was close to the long-term average for these months (Table 2). However, rainfall in December, January and February was 92% lower than the long-term average. And, rainfall from April through July, 1999 was 77% lower than the long-term average. Air temperature from January through June, 1999 was markedly higher than the 40-year average (Table 2).

Mean monthly branch elongation is shown among species, months and sites in Table 3. Analysis of variance (*ANOVA*) showed significant variation in branch elongation among months in all species (Table 4), but there was no significant variation in branch elongation among months in black brush at the CR site or in Texas ebony at the SAN site.

In guajillo, 63.1% of the increase in branch length occurred in November, December and January at the YBT site and 69.1% of the growth occurred in these same three months at the SAN site. Much of

Table 3. Comparison of mean branch elongation (cm) per month among months, species, and study sites. $N = 10$ for each mean. Numbers in parenthesis equal one standard error of the mean. Sp = species, *A. b.* = *Acacia berlandieri, A. f.* = *Acacia farnesiana, A. r.* = *Acacia rigidula, A. s.* = *Acacia schaffneri, C. e.* = *Chloroleucon ebano,* CR = Castilla Ranch, SAN = Santa Ana National Wildlife Refuge and YBT = Yturria Brush Tract.

Sp & Site	Nov 98	Dec 98	Jan 99	Feb 99	Mar 99	Apr 99	May 99	Jun 99	Jul 99	Aug 99
A. b.	3.67	1.91	1.38	0.02	0.06	0.73	0.93	1.07	0.44	0.79
YBT	(0.72)	(0.70)	(0.52)	(0.02)	(0.03)	(0.27)	(0.51)	(0.70)	(0.19)	(0.35)
A. b.	4.44	3.01	0.84	0.88	0.92	0.50	1.05	0.01	0.34	0.00
SAN	(0.58)	(1.41)	(0.52)	(0.46)	(0.55)	(0.26)	(0.62)	(0.01)	(0.34)	(0.00)
A. f.	7.82	0.13	0.10	0.33	0.22	2.40	2.75	0.41	0.15	0.29
CR	(1.01)	(0.11)	(0.07)	(0.19)	(0.16)	(1.16)	(1.32)	(0.28)	(0.15)	(0.28)
A. f.	9.04	1.82	0.83	0.00	0.08	3.87	0.34	0.49	0.89	1.41
SAN	(1.69)	(1.59)	(0.45)	(0.00)	(0.08)	(1.74)	(0.16)	(0.40)	(0.71)	(1.01)
A. r.	4.45	1.73	0.12	0.64	0.49	2.14	3.92	1.19	4.83	3.20
CR	(1.07)	(1.69)	(0.07)	(0.40)	(0.33)	(0.98)	(1.28)	(0.62)	(1.73)	(1.19)
A. r.	5.31	1.05	0.19	0.01	0.23	0.35	0.12	0.04	0.02	1.23
YBT	(0.91)	(0.42)	(0.12)	(0.01)	(0.20)	(0.19)	(0.12)	(0.04)	(0.01)	(0.88)
A. r.	4.52	1.13	0.31	0.18	0.18	2.21	0.45	1.24	0.46	1.15
SAN	(1.11)	(0.50)	(0.21)	(0.15)	(0.16)	(0.80)	(0.21)	(0.59)	(0.38)	(0.60)
A. s.	1.10	1.07	0.41	2.87	2.47	2.27	5.10	0.24	0.10	2.35
CR	(0.51)	(0.59)	(0.25)	(1.25)	(0.69)	(0.97)	(1.47)	(0.20)	(0.06)	(1.25)
A. s.	1.34	0.00	0.34	0.86	6.95	2.78	2.93	0.15	0.06	0.06
YBT	(1.09)	(0.00)	(0.35)	(0.70)	(1.90)	(1.70)	(1.41)	(0.07)	(0.04)	(0.05)
C. e.	2.89	0.14	0.45	0.04	0.13	2.36	1.95	0.11	0.02	3.61
YBT	(0.86)	(0.09)	(0.42)	(0.04)	(0.13)	(1.01)	(0.73)	(0.09)	(0.01)	(1.61)
C. e.	0.45	1.67	0.01	0.10	0.00	1.69	0.29	0.54	0.41	0.39
SAN	(0.45)	(0.77)	(0.01)	(0.07)	(0.00)	(1.12)	(0.19)	(0.33)	(0.35)	(0.33)

the growth in branch length took place in November alone in huisache (53.6% at the CR site and 48.2% at the SAN site). Increase in branch length was concentrated in November and December in black brush at two of the three sites (74.4% at the YBT site, 47.8% at the SAN site). Branch elongation at the CR site was distributed more evenly among months, but was low in January, February and March.

Branch elongation in huisachillo showed a very different seasonal pattern than the other three *Acacia* species. At both the CR site (70.7%) and the SAN site (87.4%) most of the growth occurred in late winter and spring, i.e., February, March, April and May. In Texas ebony, branch elongation was distributed at peaks throughout the ten months. At the YBT site growth was concentrated in November, April, May and August, while at the SAN site growth was greatest in December and April.

Table 4. Analysis of Variance of mean monthly branch elongation among species and sites. CR = Castilla Ranch, YBT = Yturria Brush Tract and SAN = Santa Ana National Wildlife Refuge. DF = degrees of freedom, SS = Sums of Squares, MS = Mean Squares, F = *ANOVA* value. NS = Not Significant ($P > .05$), * = $P < .01$, ** = $P < .001$.

Species and Site	Source	DF	SS	MS	F
Acacia berlandieri	Among months	9	99.368	11.041	39.573**
YBT	Within months	90	25.122	0.279	
Acacia berlandieri	Among months	9	193.913	21.546	6.069**
SAN	Within months	90	319.517	3.550	
Acacia farnesiana	Among months	9	536.198	59.575	13.680**
CR	Within months	90	391.198	4.355	
Acacia farnesiana	Among months	9	686.108	76.234	7.371**
SAN	Within months	90	930.789	10.342	
Acacia rigidula	Among months	9	70.136	7.793	0.562 NS
CR	Within months	90	1,247.210	13.858	
Acacia rigidula	Among months	9	237.293	26.367	14.017**
YBT	Within months	90	169.315	1.881	
Acacia rigidula	Among months	9	160.316	17.813	5.754**
SAN	Within months	90	278.645	3.096	
Acacia schaffneri	Among months	9	212.858	23.651	3.192*
CR	Within months	90	666.922	7.410	
Acacia schaffneri	Among months	9	433.642	48.182	4.683**
YBT	Within months	90	925.927	10.288	
Chloroleucon ebano	Among months	9	173.204	19.245	3.779**
YBT	Within months	90	458.286	5.092	
Chloroleucon ebano	Among months	9	34.732	3.859	1.582 NS
SAN	Within months	90	219.555	2.440	

Correlation between mean monthly branch elongation and the previous month's rainfall is compared between species and sites in Table 5. This correlation allows time for growth after rainfall occurs. Guajillo, huisache and black brush showed significant positive correlations at one or two sites. Huisachillo and Texas ebony did not have significant correlations with the previous month's rainfall. There were no significant correlations in any species between mean monthly branch elongation and mean monthly temperature. Only guajillo at the SAN site showed a significant correlation between mean monthly branch elongation and mean monthly photoperiod ($r = -0.682$, 8 *df*, $P < 0.05$).

Mean branch elongation over the 10 months of study was used to compare growth between sites within species. Guajillo, huisache and huisachillo did not exhibit significant variation between sites. Conversely, black brush had significant variation among the three sites where it was studied ($F = 11.897$, 2 & 27 *df*, $P < 0.001$). The SAN

Table 5. Correlation coefficients for mean monthly branch elongation versus the previous month's rainfall. $N = 10$ for all species and locations. CR = Castilla Ranch, YBT = Yturria Brush Tract and SAN = Santa Ana National Wildlife Refuge. NS = not significant ($P > .05$). * = $P < .05$, ** = $P < .01$.

Species	CR	YBT	SAN
Acacia berlandieri		0.715 *	0.563 NS
Acacia farnesiana	0.739 *		0.884 **
Acacia rigidula	0.304 NS	0.688 *	0.923 **
Acacia schaffneri	- 0.324 NS	- 0.116 NS	
Chloroleucon ebano		0.385 NS	0.554 NS

site had greater mean branch elongation than the YBT site ($t = 2.166$, 18 *df*, $P < 0.05$) and the CR site had a greater mean than either the SAN site ($t = 2.996$, 18 *df*, $P < 0.01$), or the YBT site ($t = 4.050$, 18 *df*, $P < 0.001$). Texas ebony also showed significant variation in branch elongation between sites ($t = 2.287$, 18 *df*, $P < 0.05$).

DISCUSSION

Hypothesis 1 that there are no significant differences in the patterns of branch elongation of the *Acacia* species studied was falsified. Branch elongation occurred primarily in fall and early winter in guajillo, huisache and black brush but in huisachillo, branch elongation principally took place in late winter and spring. Eddy & Judd (2003) also found significant differences in the flowering and fruiting phenologies of these *Acacia* species.

Hypothesis 2 that variation in branch elongation among the *Acacia* species was less than the variation between any of the *Acacia* species and Texas ebony also was falsified. Huisachillo differed from the other species of *Acacia* in the timing of branch elongation (as explained above) and unlike the other *Acacia* species, huisachillo did not show a significant correlation with rainfall. It was similar to Texas ebony in this respect. Eddy & Judd (2003) found that the flowering and fruiting of these *Acacia* species were more similar to each other than to Texas ebony. Thus, the data on branch elongation are very different from that on flowering and fruiting.

Hypothesis 3 that there are no significant correlations between climatic factors and branch elongation also was falsified. Guajillo, huisache and black brush showed significant positive correlations with rainfall. Additionally, guajillo at the SAN site had a significant inverse correlation with mean monthly photoperiod. Thus, these findings support the conclusion of New (1984) that growth in *Acacia* species is often correlated with moisture. Vora (1990) stated that plant growth and reproduction were keyed to rainfall and soil moisture for most of the 19 species he studied at Santa Ana National Wildlife Refuge. Also, Nilsen & Muller (1981) found that branch elongation in the legume *Lotus scoparius* in California was primarily influenced by soil moisture and they suggested that this is a common response in chaparral plants.

These data were obtained during a drought. Rainfall from November 1998 through August 1999 in the LRGV was only about half (47.3%) of the long-term average for this time period. Clearly, the drought may have influenced the phenological responses of the species studied. Furthermore, it is possible that data for September and October, which are lacking here, might have produced different conclusions about the seasonal patterns of branch elongation since these are the two months with the greatest rainfall in the LRGV. However, this seems unlikely because there was no correlation between rainfall and branch elongation in huisachillo.

Additional information, especially from wet years, is needed to elucidate the full range of growth responses for these and other species of *Acacia* in the LRGV. This study points to the need for experiments on the effects of soil moisture on growth to help explain the differences observed between huisachillo and the other three *Acacia* species.

Among sites variation is not often assessed in phenological studies. It was shown that this was an important factor in two of the five species studied. In arid environments, variation in soil moisture is common both within and between sites (Beatley 1974) and it may be the proximate cause of variation in phenological responses in this study.

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GENERAL NOTES

SYSTEMATIC AND ECOLOGICAL NOTES ON *TUBIFICOIDES HETEROCHAETUS* (OLIGOCHAETA: TUBIFICIDAE) FROM THE NECHES RIVER ESTUARY, TEXAS

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Tubificoides heterochaetus (Michaelsen 1926) is an estuarine oligochaete in the Family Tubificidae that has been reported in Europe and North America. North American records include Virginia, North Carolina, Florida, Louisiana and the Sabine-Neches estuary in Texas (Wern 1980; Shirley & Loden 1982; Harrel & Hall 1991; Milligan 1996; Harrel & Smith 2002). All of the publications concerning this species, except Shirley & Loden (1982), are taxonomic, and no information is given concerning its water quality tolerance.

The taxonomic status of this species was in a state of confusion until recently. It was originally described by Michaelsen (1926) and placed in the genus *Limnodrilus* and later transferred to the genus *Peloscolex* (Lastockin 1937; Cekanovskaya 1962; Brinkhurst & Jamison 1971). Holmquist (1978) established the genus *Tubificoides* and in 1979 Brinkhurst & Baker transferred the marine and estuarine *Peloscolex* to the genus *Tubificoides*.

Descriptions of *T. heterochaetus* in the literature vary from one author to another and most were based on specific lectotypes and did not consider all of the morphological variation that occur in the species. *Tubificoides heterochaetus* was originally described by Michaelsen (1926) as possessing a cuticular penis sheath. Brinkhurst & Jamison (1971) and Brinkhurst & Baker (1979) described it as lacking a penis sheath. Baker (1981) redescribed the species to correct this. Milligan (1996) contains the only taxonomic key, known by this author, that can be used by an applied biologist for proper identification of *T. heterochaetus*. However, numbers of setae per bundle, lengths of setae, and width and length of the penis sheath vary more than the scattered literature states. Thus, an updated description of the species is given based on the literature and examination of 302 specimens collected from the Neches River estuary in Texas. The diagnostic characteristics of the genus are based on histological genitalia structures and these are not often visible in specimens collected and prepared for ecological purposes. Thus, the description below is based on structures visible without special handling or dissection. All specimens examined were killed and preserved in formalin containing rose bengal stain, stored in 70 percent ethanol and mounted in CMC-10 media on microscope slides.

Complete specimens 5 to 9 mm long and ranged from 46 to 66 segments, but most were incomplete. Maximum width ranged from about 375 to 500 μm at segment X or XI. Anterior segments (I-XII) are non-papillate and distinctly wider than posterior papillate segments which are 70 to 160 μm wide (Figure 1). The posterior papillate segments are elongate and often constricted at their base. The prostomium is conical and shorter or equal to its base at the peristomium. Anterior segments II through XII become progressively longer. Segments II through IX have secondary annulations and have 3 to 8 (mostly 5 or 6) 38 to 50 μm long ventral and dorsal bifid setae per bundle with equal length teeth. Segment IX may have one, two or no setae. Clitellar segments X, XI and XII lack setae. A short thimble-shaped penis ranging from 36 to 37 μm wide at the base and 37 to 46 μm long with a thin cuticular sheath may be present in or just outside of segment XI. Only eight of 302 specimens examined had a visible penis sheath; two collected in February, two in May, one in August and three in November. Segment XIII decreases in width from anterior to posterior and scattered papille first appear. Segments behind XIII are covered with oblong papillae, but the posterior segments of complete specimens had very few or lacked papillae. Some post-clitellar segments possess 1, 2 or occasionally 3 apparently simple pointed setae per bundle 54 to 67 μm long. Some posterior setae are actually bifid and the upper tooth is longer and thicker than the shorter, thinner lower tooth, which is not visible unless turned just right. The posterior setae are often broken, difficult to see or absent in some segments. If all of the papillate segments of a specimen are missing it could easily be misidentified as *Limnodrilus*.

Harrel et al. (1976), Harrel & Hall (1991) and Harrel & Smith (2002) conducted three year-long surveys, with seasonal sampling of macrobenthos at the same seven collection stations in the highly industrialized, tidal, lower Neches River. A 1971-72 study (Harrel et al. 1976) was conducted before implementation of the Clean Water Act (CWA) when this section of the river was listed as the second most polluted waterway in the state with a permitted BOD (biochemical oxygen demand) waste load of 123,125 kg/day. Oxygen depletion (concentrations <2 mg/L)

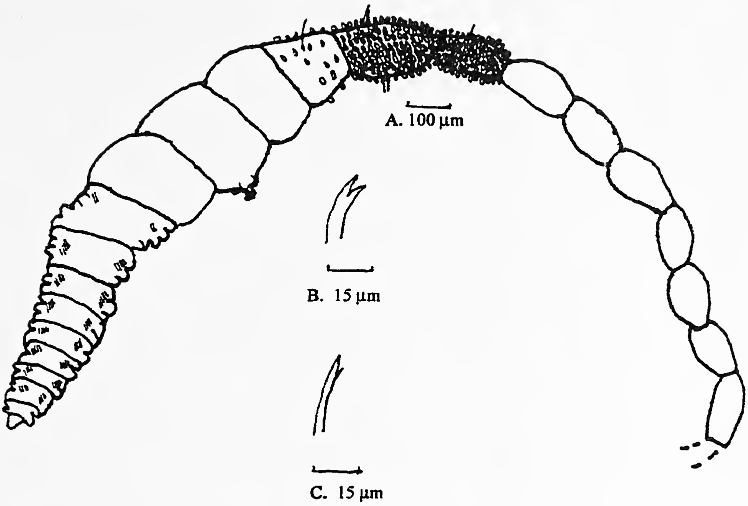

Figure 1. *Tubificoides heterochaetus*: (a) body, (b) tip of anterior and dorsal seta, and (c) tip of posterior weakly bifid seta.

occurred at all stations and toxic pollutants were present in the water and the substrate. No *T. heterochaetus* were collected during this survey and they may have been excluded by the heavy load of organic and toxic pollutants in the river.

During a 1984-85 study (Harrel & Hall 1991), after implementation of the first two phases of the CWA and a 93 percent reduction in the permitted BOD pollution load in the river to 8,717 kg/day, a total of 525 specimens of *T. heterchaetus* were collected from six of the seven sampling stations. Density at individual collection stations ranged from zero to 1196/m^2 and maximum density occurred during February. Salinity ranged from <0.5 ppt to 8.5 ppt at the stations and depths where it occurred.

During a 1999 study (Harrel & Smith 2002), after implementation of phase 3 of the CWA, but a 19 percent increase in the permitted BOD waste load in the river, 302 specimens of *T. heterochaetus* were collected at five of the seven collecting stations. Density at individual collecting stations ranged from zero to 991/m^2 and maximum density occurred in November. Salinity ranged from <0.5 ppt to 13.2 ppt.

During 1978 and 1979 Wern (1980) conducted monthly collections of macrobenthos from 12 stations in the Keith Lake system of marsh lakes located between the Sabine-Neches navigation channel, the Gulf of Mexico and the Intracoastal Waterway. She collected 1254 specimens of *T. heterochaetus* and some specimens were collected at all 12 stations at some time during the study. Density ranged from zero to $3075/m^2$ and highest densities occurred during July and August, which was attributed to a reproductive event. Salinity ranged from <0.5 to 20 ppt. Mean station bottom water dissolved oxygen concentrations ranged from 6.0 to 7.1 mg/L. No permitted effluents were released directly into this system, but some contaminants (e.g., metals, oil and grease) were present in the sediments and were probably transported in by tidal action from the Intracoastal Waterway and the Sabine-Neches Navigation channel or from oil field activity in the area. These occurred in higher concentrations at some stations than at others, but no differences in macrobenthos distribution, abundance or diversity could be attributed to pollution.

Shirley & Loden (1982) reported *T. heterochaetus* from the Calcasieu River estuary in Louisiana, which is located about 80 km east of the Neches River and Keith Lake estuaries. Specimens were collected from 10 of 27 stations sampled during 1974 to 1976. No specimens were collected at stations where oxygen depletion occurred and environmental parameters where they were collected included: (1) salinity - 2.3 to 14.1 ppt, (2) oxygen percent saturation - 68 to 112%, (3) depth - 1.0 to 5 m, and (4) substrate - clay and silt. Density rarely exceeded $100/m^2$ and average density was $46.2/m^2$.

Other Oligochaetes that occurred with *T. heterochaetus* in the Neches River and Keith Lake estuaries include *Limnodrilus hoffmeisteri*, *L. udekmianus*, *Ilyodrilus templetoni*, *Aulodrilus piguetti*, *A. pluriseta*, *Dero nivae*, *D. furcata*, *Slavinia appendiculata*, *Nais variabilis* and *Paranais grandis*. All of these are considered freshwater species, except *P. grandis* which has been reported only from coastal Louisiana and Texas. Polychates that were common where *T. heterochaetus* occurred were *Hobsoni grayi*, *Parandalia americana*, *Neanthes succine*, *Laeonereis culveri*, *Polydora socialis*, *Streblospio benedicti* and *Mediomastus californiensis*.

Tubificoides heterochaetus is a oligohaline to mesohaline estuarine species restricted to habitats where the salinity varies from <0.5 to 20 ppt, but was uncommon where salinity was <2 ppt or >14 ppt. It occurred in sand, silt and clay substrates and at depths to at least five meters. It is tolerant to moderate pollution and cannot tolerate oxygen depletion or severe pollution. It was not collected in the Neches River estuary until after pollution abatement occurred resulting in improved water quality when it became a common component of the benthic community.

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REPRODUCTION IN THE WESTERN HOGNOSE SNAKE, *HETERODON NASICUS* (SERPENTES: COLUBRIDAE) FROM THE SOUTHWESTERN PART OF ITS RANGE

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The western hognose snake, *Heterodon nasicus* ranges from southern Canada to San Luis Potosí, México and southeastern Arizona to central Illinois where it frequents prairies, open woodlands and floodplains of rivers; in the extreme western part of its range it occurs in semidesert habitats (Stebbins 2003). Most of the information on reproduction in this species was reported by Platt (1969) who studied a Kansas population of *H. nasicus*. Anecdotal information on reproduction is in: Marr (1944); Werler (1951); Moore (1953); Wright & Wright (1957); Fitch (1970); Pendlebury (1976); Tennant (1984); Lowe et al. (1986); Taggart (1992); Iverson (1995); Degenhardt et al. (1996) and Stebbins (2003). Ernst & Ernst (2003) summarized information on reproduction in *H. nasicus*. Information on the biology of this species is in Walley & Eckerman (1999). The purpose of this paper is to present the first reproductive data on *H. nasicus* from the southwestern part of its range based on a histological examination of reproductive tissues from museum specimens. Studying the reproductive cycle in different parts of a snake's range allows one to see the extent of geographic variation in reproduction within a species. Also presented is the first histological evidence that *H. nasicus* females initiate yolk deposition (= secondary vitellogenesis *sensu* Aldridge 1979) during late summer in follicles that will be ovulated the following year.

A sample of 37 specimens of *H. nasicus* (19 females, mean snout-vent length, SVL = 480.4 ± 71.3 *SD*, range: 361-613; 18 males, SVL = 324.3 mm ± 34.9 *SD*, range: 290-390 mm) from Arizona, New Mexico and México was examined from the herpetology collections of Arizona State University (ASU), the Natural History Museum of Los Angeles County, Los Angeles (LACM) and the University of Arizona, Tucson (UAZ). Most snakes (33/37) 89% were from Arizona. Snakes were collected 1949-1999. Counts were made of enlarged follicles > 8 mm length or oviductal eggs. The left testis, vas deferens and a portion of the kidney were removed from males; the left ovary was removed from females for histological examination (except for females with enlarged follicles or oviductal eggs which were counted). Tissues were embedded in paraffin and sectioned at 5 μm. Slides with tissue sections were stained with Harris' hematoxylin followed by eosin counterstain. Testes slides were examined to determine the stage of the male cycle; ovary slides were examined for the presence of yolk deposition (secondary yolk deposition *sensu* Aldridge 1979). Some snakes were road-kills so not all tissues were available for examination. Number of specimens histologically examined by reproductive tissue were: testis = 18, vas deferens = 16, kidney = 18, ovary = 16. Male and female mean body sizes were compared using an unpaired *t*-test.

Table 1. Monthly distribution of conditions in seasonal testicular cycle of *Heterodon nasicus* from examination of museum specimens. Values shown are the numbers of males exhibiting each of the three conditions.

Month	*n*	Regressed	Recrudescence	Spermiogenesis
May	1	1	0	0
June	1	1	0	0
July	1	0	1	0
August	2	0	0	2
September	6	0	0	6
October	7	0	0	7

Material examined.—The following specimens of *Heterodon nasicus* were examined: ARIZONA: COCHISE COUNTY, (ASU 22859, LACM 109514, 115794, 145667, UAZ 9365, 24934, 24935, 24937, 24938, 24941, 24942, 35159, 39611, 39612, 39617, 39618, 40146, 41146, 41147, 41152, 43892, 46321, 46322, 46833, 48011, 50017, 51822) GRAHAM COUNTY, (ASU 7029, 22461) SANTA CRUZ COUNTY, (UAZ 40778, 43756, 43799, 50066). NEW MEXICO: HIDALGO COUNTY, (ASU 31499) LUNA COUNTY, (LACM 109527). MÉXICO: CHIHUAHUA, (UAZ 39198, 39199).

Testicular histology was similar to that of the two colubrid snakes, *Masticophis taeniatus* and *Pituophis catenifer* (= *P. melanoleucus*) as reported by Goldberg & Parker (1975). In the regressed testes, seminiferous tubules contained spermatogonia and Sertoli cells. In recrudescence (recovery) there was renewal of spermatogenic cells characterized by spermatogonial divisions; primary and secondary spermatocytes were typically present. In spermiogenesis, metamorphosing spermatids and mature sperm were present. Testes undergoing spermiogenesis were found August-October (Table 1). Testes from the two spring males (one from May and one from June) were regressed. The smallest reproductively active male (spermiogenesis in progress) measured 290 mm SVL (UAZ 46322). Platt (1969) found motile spermatozoa in cloacal smears of 3/7 (43%) *H. nasicus* < 300 mm SVL from Kansas. As was the case for Kansas (Platt 1969), *H. nasicus* from the southwestern extreme of its range undergoes a postnuptial spermatogenesis = aestival spermatogenesis (*sensu* Saint Girons 1982) which is completed before winter with sperm stored over winter in the vas deferens. All vasa deferentia ($n = 16$) contained sperm: May (1), August (2), September (6), October (7). Tubules of all kidney sexual segments, except for the one July male 17/18 (94%), were enlarged and contained secretory granules: May (1), June (1), August (2), September (6), October (7), a condition that

Table 2. Monthly distribution of conditions in seasonal ovarian cycle of *Heterodon nasicus* from examination of museum specimens. Values shown are the numbers of females exhibiting each of the four conditions; *squashed oviductal eggs, clutch could not be counted.

Month	*n*	Inactive	Early yolk deposition	Enlarged follicles > 12 mm length	Oviductal eggs
May	2	1	0	0	1
June	2	0	1	1	0
July	5	0	4	0	1*
August	2	1	1	0	0
September	6	2	4	0	0
October	2	2	0	0	0

typically coincides with breeding (Saint Girons 1982). According toPlatt (1969), the principal *H. nasicus* mating period is in the spring, although some mating may also occur in autumn.

Females were significantly larger than males ($t = 8.4$, $df = 35$, $P < 0.0001$). One female *H. nasicus* from Cochise County, Arizona with five oviductal eggs (UAZ 24941) was collected 28 May. Another, (UAZ 24938) from Cochise County, with six enlarged follicles (> 8 mm length) was collected 6 June. A third female from Cochise County collected in July (ASU 22859) contained squashed oviductal eggs that could not be counted. Females with early yolk deposition (secondary yolk deposition *sensu* Aldridge (1979) were found June-September (Table 2). This yolk deposition was in the form of a small band of discrete yolk granules. Because the yolk occupied only a limited area of the follicles it would have been unlikely for yolk deposition to have been completed during the current reproductive season. However, since Platt (1969) reported *H. nasicus* deposits eggs in August (locality not given), one must consider the possibility that in some females, yolk deposition might have been completed during the current year. However, it appears that in at least some cases *H. nasicus* females initiate yolk deposition (vitellogenesis) the summer prior to completing it. For example (Fig. 1), early yolk deposition is present in UAZ 43892, a road-kill from 31 July in which the two largest follicles had lengths of 2 mm. It is doubtful that these follicles would have completed yolk deposition in the current year. These findings agree with Ernst & Ernst (2003) who reported a complement of small follicles in *H. nasicus* females which represent ova to be matured the following year. There was a report of an August *Hypsiglena torquata* female with yolk deposition in Goldberg (2001). Whether starting yolk deposition in the

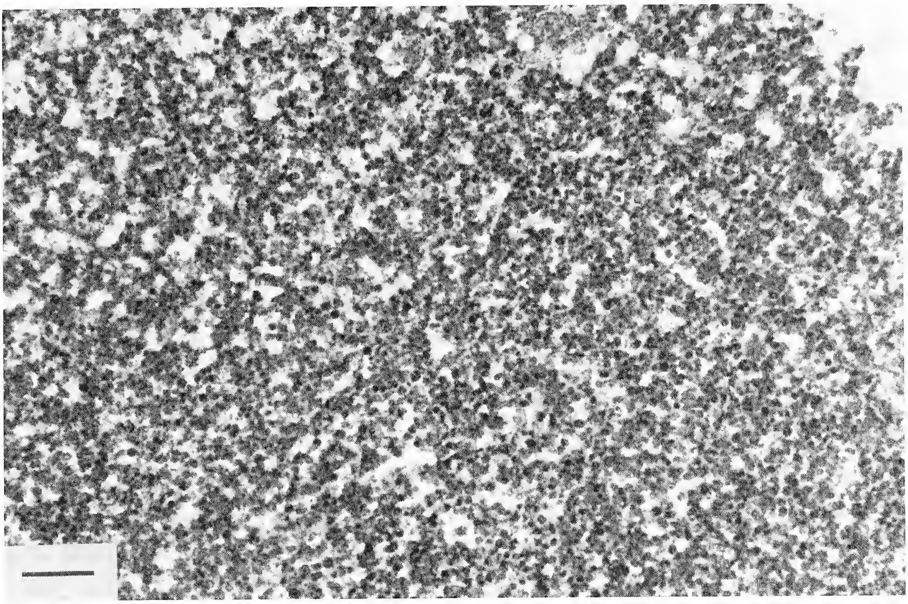

Figure 1. Yolk deposition in ovarian follicle of *Heterodon nasicus* (UAZ 43892) collected 31 July 1980. Bar represents 15 μm.

summer prior to ovulation is common in North American colubrid snakes needs to be investigated.

The two clutch sizes reported herein (5, 6) are near the lower end of the ranges for *H. nasicus* 4-23 clutch sizes reported by Platt (1969) and 4-25 reported by Stebbins (2003). The smallest reproductively active female (yolk deposition in progress, UAZ 39611) measured 361 mm SVL. This was close to the smallest gravid *H. nasicus* female (SVL = 366 mm) from Kansas (Platt 1969). Eight female *H. nasicus* from Harvey County, Kansas deposited egg clutches from 2-23 July (Platt 1969). The presence of one Arizona female *H. nasicus* (UAZ 24941) with oviductal eggs on 28 May and a female from Valencia County, New Mexico that deposited eggs on 12 June (Degenhardt et al. 1996) may suggest that females from the southern portion of the range produce eggs earlier in the year than females from the northern part. Small sample sizes prevent an analysis of geographic variation in clutch sizes, although Fitch (1985) found no evidence of geographic change in clutch sizes between northern and southern populations of *H. nasicus*.

In conclusion, there does not appear to be differences in the timing of the seasonal testicular cycle of *H. nasicus* between Kansas and the southwestern part of its range in that sperm produced in autumn are stored through winter in the vasa deferentia in both areas. There is a suggestion that eggs may be produced earlier in the season in the south. Additional females need to be examined to determine if this occurs. It appears that some *H. nasicus* females initiate yolk deposition (vitellogenesis) in follicles the summer before eggs are produced.

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ENDOPARASITES OF THE SEQUOYAH SLIMY SALAMANDER, *PLETHODON SEQUOYAH* (CAUDATA: PLETHODONTIDAE), FROM MCCURTAIN COUNTY, OKLAHOMA

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The Sequoyah slimy salamander, *Plethodon sequoyah*, is a medium-sized plethodontid that is restricted to McCurtain County, Oklahoma (Conant & Collins 1998) and perhaps adjacent Sevier County, Arkansas (Trauth et al. 2004). This salamander occurs in upland forests where it inhabits seeps and springs hiding beneath rocks, clumps of moss, or under decaying logs. This species, one of several belonging to the *P. glutinosus* group 10 complex, was described by Highton (1989) as having a unique Mdh-2 allele that distinguishes it from 15 other species of the *P. glutinosus* group. In addition, this evolutionary lineage has also been recognized by Powell et al. (1998) and Duellman & Sweet (1999), and most recently was included on a list of standard and common current scientific names (Collins & Taggart 2002).

Although information is available on parasites of other species within the *P. glutinosus* complex (Baker 1987; McAllister et al. 1993; 2002), nothing, to the authors' knowledge, has been published on protozoan or helminth parasites of *P. sequoyah*. This study provides the first report of endoparasites from this host.

Twenty-five juvenile and adult salamanders (mean ± 1 *SD* snout-vent length [SVL] = 46.5 ± 14.3, range 24-74 mm) were collected by hand, two on 13 September 2002, six on 3 June 2003, and 17 on 15 April 2004 from Beaver's Bend State Park, McCurtain County, Oklahoma (33° 7.7'N, 94° 41.9'W, elev. 153.6 m). Specimens were placed in damp collecting bags on ice and returned to the laboratory within 24h for processing. Specimens were killed by prolonged immersion in a dilute Chloretone® solution. For necropsy, a midventral incision was made and the entire gastrointestinal tract, liver, gallbladder, spleen and gonads were examined for helminths. Blood smears were taken from the exposed heart and stained with DifQuick. Feces from the colon and rectum were collected and placed in individual vials containing tap water supplemented with antibiotic (100 I. U./mL penicillin-G 100 μg/mL streptomycin) and examined directly without sucrose flotation by microscopy for coccidia. The integument was examined closely for intradermal mites (*Hannemania*). Tapeworms were relaxed in cold tap water, fixed in 70% ethanol, stained with Semichon's acetocarmine and mounted entire with Permount®. Nematodes were placed in a drop of glycerol on microscopic slides and identifications were made from these temporary mounts. Helminth voucher specimens were deposited in the United States National Parasite Collection (USNPC), Beltsville, Maryland, USA, and the Harold W. Manter Laboratory of Parasitology, Lincoln, Nebraska, USA: *Cepedietta michiganensis* (HWML 45996), *Cylindrotaenia idahoensis* (USNPC 94810, 95245), *Mesocestoides* sp. (USNPC 94811), *Batracholandros magnavulvaris* (USNPC 94812, 95246), *Cosmocercoides variabilis* (USNPC 94813). Host voucher specimens were deposited in the Arkansas State University Museum of Zoology (ASUMZ 27250, 27920-27924) and University of Oklahoma Museum of Natural History (OMNH 39181).

Eighteen of 25 (72%) of the *P. sequoyah* were infected with one of five parasite species, including one (4%) with *Cepedietta michiganensis* in the small intestine, seven (28%) with *Cylindrotaenia idahoensis* (mean intensity 6.3, range 1-19) in the small intestine, two (8%) with *Mesocestoides* sp. in the mesenteries and peritoneal cavity, three with *Cosmocercoides variabilis* (mean intensity 9.7, range 5-17, 13 females, 16 males) in the rectum, and eight (32%) each with a single female of *Batracholandros magnavulvaris* in the rectum; six salamanders (24%) harbored multiple infections. Blood smears were negative for hematozoa, the feces did not contain coccidia, and none of the salamanders were infested with *Hannemania*.

The astomatous ciliate, *C. michiganensis* has been reported previously from various salamanders and frogs (Joy & Tucker 2001; McAllister & Bursey 2004), including the Fourche Mountain salamander, *P. fourchensis*, western slimy salamander, *P. albagula*, and Rich Mountain salamander, *P. ouachitae* from Arkansas (Winter et al. 1986; McAllister et al. 1993; 2002), and the southern redback salamander, *P. serratus* from Oklahoma (McAllister et al. 2002). This study represents the first report of this protist in *P. sequoyah.*

The cyclophyllidean tapeworm, *C. idahoensis* was originally described from the Coeur d'Alene salamander, *P. idahoensis* from Idaho (Waitz & Mehra 1961). Since then, this cestode has been reported in Jordan's redcheek salamander, *P. jordani* from North Carolina (Dyer 1983; Jones 1987), the western redback salamander, *P. vehiculum* from Oregon (Panitz 1969), and the Caddo Mountain salamander, *P. caddoensis, P. ouachitae* and *P. serratus* from Arkansas and Oklahoma (McAllister et al. 2002). This study documents a new host record for the parasite in *P. sequoyah.*

The cestode, *Mesocestoides* sp. is an enigmatic tapeworm whose complete life cycle is unknown. The initial report in salamanders of the world was by McAllister et al. (1995) who reported this parasite in eight of 41 (20%) Ouachita dusky salamanders, *Desmognathus brimleyorum* from Arkansas. This study reports a second salamander host for this tapeworm. This cestode has also been previously reported from various anurans (McAllister & Conn 1990).

The ascarid nematode, *C. variabilis* has been commonly reported from both amphibians and reptiles in the United States and Canada (summarized by McAllister & Bursey 2004). This parasite (as *Oxysomatium* sp.) has also been previously reported from Oklahoma in bullfrogs, *Rana catesbeiana* (Trowbridge & Hefley 1934); however, this study reports a new host for this roundworm.

The nematode, *B. magnavulvaris* is a pinworm with a direct life cycle that exhibits little host specificity. It has been previously reported in *P. caddoensis, P. fourchensis, P. ouachitae, P. serratus* and *D. brimleyorum* in Arkansas and Oklahoma (Winter et al. 1986; McAllister et al. 1995; 2002). In addition, this parasite has a wide geographic range as it has been reported in salamanders of the genera *Aneides, Desmognathus, Eurycea, Leurognathus, Notopthalmus* from California, Illinois, Michigan, New Hampshire, North Carolina, Pennsylvania, Tennessee, Virginia and West Virginia (see Joy & Tucker 2001 for summation). *Plethodon sequoyah* represents a new host for this parasite.

In summary, although no new geographic records are documented, this study provides the first report of endoparasites from *P. sequoyah*. Several parasite species reported herein are shared with other *Plethodon* sp., and as in previous surveys on salamanders, this limited data supports Aho's (1990) suggestion that the parasite community structure is depauperate and noninteractive.

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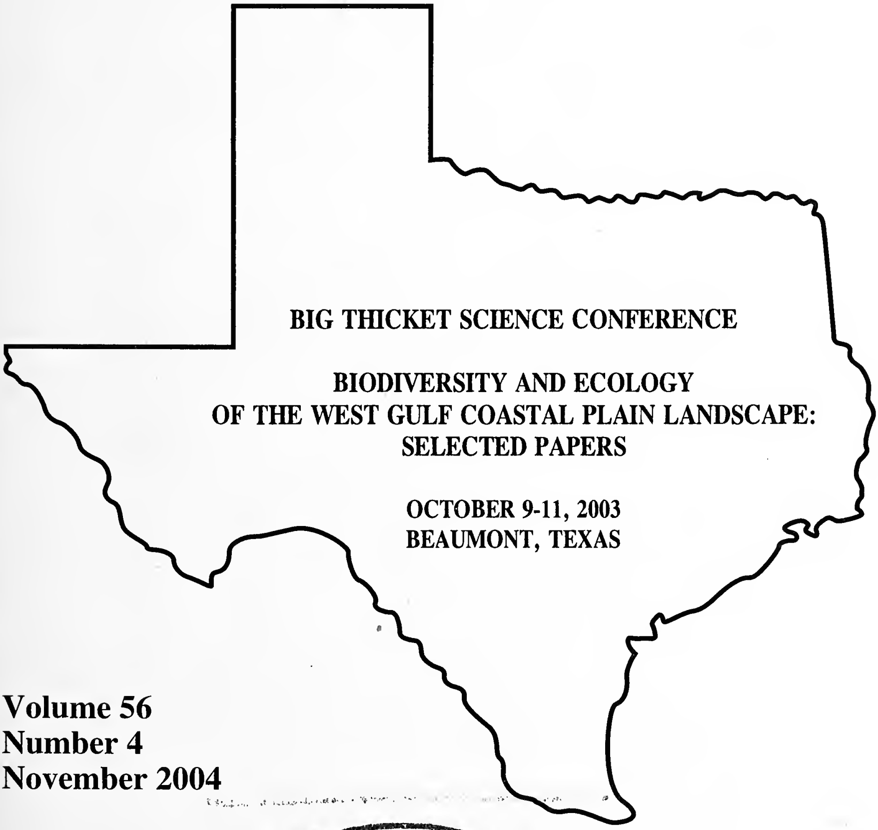

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BIODIVERSITY AND ECOLOGY OF THE WEST GULF COASTAL PLAIN LANDSCAPE: SELECTED PAPERS

OCTOBER 9-11, 2003
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Volume 56
Number 4
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The 3rd Big Thicket Science Conference, "Biodiversity and Ecology of the West Gulf Coastal Plain Landscape", was held October 9-11, 2003 in Beaumont, Texas. The Big Thicket is a biologically rich area within the West Gulf Coastal Plain where the influences of southeastern swamps, eastern deciduous forests, central plains, pine savannas and xeric sandhills meet and intermingle. The region provides habitat for many rare species and favors unusual combinations of plants and animals. The purpose of the Big Thicket Science Conference is to highlight the results of recent ecological research and conservation efforts to understand, manage and restore the unique biological diversity of the Big Thicket and surrounding West Gulf Coastal Plain. The event brought together a diverse group of individuals representing government, academia, conservation organizations, private industry and local residents.

It took the efforts of many people to produce this document. Numerous people reviewed the manuscripts included in this volume. We appreciate their input that greatly improved the quality of the manuscripts and their willingness to review manuscripts in a short period of time. We thank the contributing authors for their patience with the editorial process. We thank the *Texas Academy of Science* for their support of this project. We are particularly grateful to Ned Strenth for his assistance as managing editor. We hope this publication increases our understanding of the biological resources of this region.

The 4th Big Thicket Science Conference is scheduled for Fall 2007. Information regarding this event will be forwarded to registered participants of the 3rd conference. Other interested parties may contact: Chief of Resources Management, Big Thicket National Preserve, 3785 Milam, Beaumont, Texas 77701 (phone: 409.839.2689).

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TEXAS J. SCI. 56(4):285-298 NOVEMBER, 2004

POTENTIAL CAUSES OF A DECLINE IN AMERICAN BEECH (*FAGUS GRANDIFOLIA* EHRH.) IN WIER WOODS, TEXAS

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Abstract.—In a mature southern mixed hardwood stand in Hardin County, Texas, American beech (*Fagus grandifolia*) declined in basal area by 38% between 1985 and 2001, and 59% of the largest trees (>45 cm dbh) died (4.10%/yr). The mortality rate was nearly triple that of understory trees (4.5-14cm dbh) (1.13%/yr). Mortality increased in 1987 following a hurricane, and remained high for the 15-year duration of the study. Dead trees were aggregated in space, causing the population to change in distribution from regular to random. Evidence for pathogen damage was mostly circumstantial. Night-time temperatures, to which beech is susceptible, have been increasing over the last 20 years. No single factor (increasing temperatures, moderate hurricane damage, or pathogens) alone appears sufficient to explain the decline of large American beech trees in this forest over the past 20 years. Instead, a combination of factors seems most likely.

Southern mixed forests contain an unusually high diversity of woody plant species (Marks & Harcombe 1975). In general, they exhibit a successional trend towards dominance by beech and magnolia (Gano 1917; Kurz 1944; Glitzenstein et al. 1986), though the mixed species nature of these southern hardwood forests is hypothesized to result from complex disturbance regimes (Glitzenstein et al. 1986; Platt & Schwartz 1990). In addition to its shade tolerance and longevity, American beech may also be resistant to exogenous damage caused by tropical storms (Batista et al. 1998; Batista & Platt 2003). Consequently, beech-dominated forests might be expected to be relatively stable. However, a beech population in southeast Texas showed substantial decline between 1987 and 1999 (Harcombe et al. 2002). In this paper, the decline is analyzed and several hypotheses are tested to explain it.

One possible explanation could be a hurricane which hit the site in 1986. Within southern mixed hardwood forests, hurricanes can slow the replacement of shade-intolerant species by shade tolerant species (Glitzenstein et al. 1986; Cain & Shelton 1995; Arevalo et al. 2000). Peters & Poulson (1994) suggested that hurricanes may limit beech dominance in beech forests around the world. However, there is also contrary evidence; hurricanes did not strongly reduce American beech growth rates in northern Florida (Batista et al. 1998) or in east Texas (Bill 1995).

Another possible explanation involves climate change. Recent modeling research indicates that American beech distribution within the United States is governed by temperature, precipitation, soil, and elevation-related variables (Iverson & Prasad 1998). Box et al. (1993) define the climatic space corresponding to the geographic species range as a "climate envelope." The envelope for American beech involves, among other measures, a relatively moist climate and maximum daily temperatures between 17°C and 29°C. Davis & Zabinski (1992) modeled the distribution of American beech with respect to temperature and predicted that if temperature increased, species at their southern range limits, including American beech, would exhibit immediate declines in seedling density and an eventual decline of canopy trees after a few decades of warming. Other studies in North America have also suggested that increasing summer temperature significantly reduces American Beech growth (Fritts 1958; Tubbs & Houston 1990, Tardiff et al. 2001). Finally, a recent dendroecological study in Texas showed high sensitivity of American beech to temperature and precipitation between the summer months of May and July (Cook et al. 2001). Particularly in east Texas, where American beech reaches its southwestern range limit, increasing summer temperatures may exceed heat tolerance limits of the species, affecting growth and mortality.

American beech is also vulnerable to sucking insects, decay fungi, and pathogens (Tubbs & Houston 1990). The most notorious example is Beech Bark Disease, which has affected American beech trees in the northeastern United States (Ehrlich 1934; Houston et al. 1979). In the southern United States, the bark canker fungus *Hypoxylon atropunctatum* has been documented on American beech trees (Thompson 1963; Pase 2002). *Hypoxylon* first affects the cambium; it is thought to be triggered by low moisture in the xylem and can take three to four years to kill a tree (Pase 2002). Aphid infestation can also damage beech; it has recently been documented in east Texas (Hemmingsen 2002; Siemann & Rogers 2003).

A variety of abiotic and biotic factors clearly influence American beech populations. Declines of woody species could also be related to species population structure and natural population dynamics (reviewed in Mueller-Dombois 1992). Furthermore, population dynamics may be strongly influenced by the series of stresses each individual in a population experiences. Manion (1981) classified stresses into two categories: "predisposing factors," which are long term stresses, and "inciting factors," which are short-duration stresses. Pederson (1998) showed that trees with a negative response to a prior stress were more likely to have a negative response to a subsequent stress. Thus, tree mortality can be the result of a variety of factors that act over a lifetime, and growth and mortality may be synchronized in a population that has a history of stresses.

The hurricane, changing climate conditions, and pathogens could be acting together or separately, along with stress history or population structure, to cause the decline of American beech in Wier Woods. In this paper, these hypotheses are examined by analyzing 22 years of data on spatial and temporal variation in beech growth, recruitment, and mortality.

STUDY SITE

The study site is a 4 ha plot in Wier Woods Preserve (The Nature Conservancy), located about 16 km north of Beaumont, Hardin County (30°16' N, 94°12' W), Texas (Figure 1). Wier Woods is located 140 km east of the western range limit of the species (McLeod 1975), just 5 km north of the southern range limit for American beech (Little 1971). The site is part of the Big Thicket (Marks & Harcombe 1981), a 2500 km^2 forested region located 50-100 km inland from the Gulf of Mexico. The soil is a siliceous, thermic, Susquehanna fine sandy loam (Deshotels 1978). Average annual temperature is 20.4°C, with a long growing season (approx. 240 days) from March to November (Harcombe et al. 2002). Species composition in the Wier Woods is typical of southern mesic forests (Quarterman & Keever 1962; Blair & Brunett 1976; Glitzenstein, et al. 1986). The important species in Wier Woods include loblolly pine *(Pinus taeda)*, water oak (*Quercus nigra*), American beech (*Fagus grandifolia*), southern magnolia (*Magnolia grandiflora*), and white oak (*Quercus alba*) (Harcombe et. al. 1998). Glitzenstein et al. (1986) found that disturbance at Wier Woods may accelerate early successional stands of pine and oak towards beech and magnolia dominance and also re-initiate new regeneration of pine and oak in areas currently dominated by beech and magnolia. Harcombe et al. (2002) noted the rapid decline in basal area of beech, in spite of increases in most other species and an overall increase in stand basal area.

On June 26, 1986, Hurricane Bonnie, with winds estimated at 120 km/hr, passed over the site (Doyle & Girod 1997; NOAA 1986).

METHODS

Data for this research are from a permanent sample plot of approximately 4 ha. An irregular polygon was divided into 101 contiguous 20 by 20 m cells, and stems with DBH $>$ 4.5 cm were tagged and mapped; species identity and DBH was measured for each stem. All

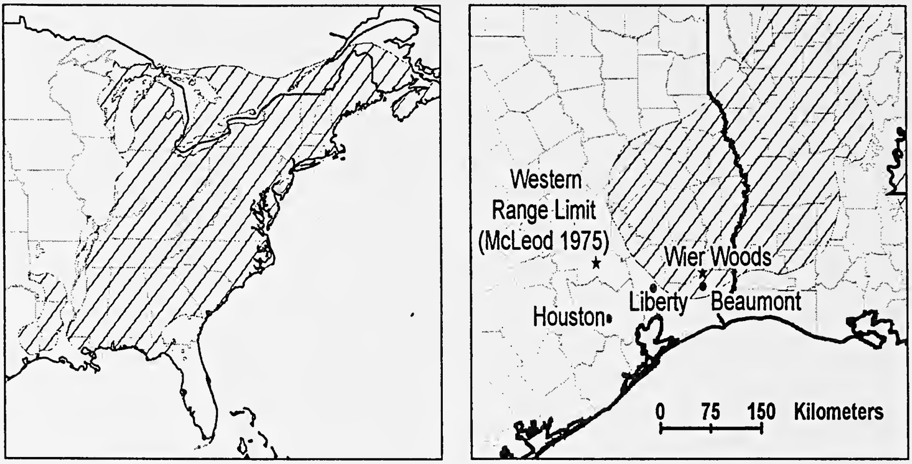

Fig. 1. American beech distribution in southeastern U.S.A. (Little 1971).

tagged trees were measured in May or June of 1980, 1982, 1985, 1987, 1989, 1992, 1995, 1998, and 2001. All stems that had reached 4.5 cm DBH since the last measurement (ingrowth) were tagged and mapped.

Trees with missing or anomalous DBH values were assigned an interpolated value. Trees missed in earlier surveys were assigned DBH values by back projection, based on calculated mean growth rates for the appropriate time period, species, size, and class (Bill 1995). All of the interpolated values were used in calculations of basal area and density, but not in calculations of growth rates, even though they had only a small effect on growth values. Data were analyzed using SAS (SAS Institute) or Microsoft Excel (ver. MS2000). Average annual growth rates were calculated by dividing change in DBH by the number of years between measurements.

Mortality surveys were conducted annually, and percent mortality was calculated as the number of individuals found dead in a single year divided by the number of individuals in the living population in the previous year. The possible existence of a temporal pattern in mortality (as opposed to a random fluctuation) was evaluated by comparing two models of large beech mortality using the Akaike Information Criteriron or AIC (Burnham & Anderson 2002). The AIC incorporates both the likelihood of the data given in the model, and the number of free parameters in the model; the model with the lowest AIC is considered to be the best supported by the data. The first model assumed a constant probability of mortality, with the average mortality rate as the one free parameter. The second model approximated mortality by a step function, with one probability before and one probability after the step. For this model there were three free parameters: the first and second mortality probabilities and the time of the step between the two.

Mortality as a function of DBH was also predicted with logistic regression using the Weibull distribution (Antle & Wain 1988). Models were fitted for the intervals six years before Hurricane Bonnie (1981-1986), the year immediately after the hurricane (1987), six years after the hurricane (1987-92), and the 14 years after the hurricane (1987-2001).

The Clark-Evans Nearest Neighbor Test (Clark & Evans 1954) was used to test for aggregation of the American beech population. Because distributions at any time are highly influenced by the prior population distribution, a randomization test was also performed to determine whether mortality was aggregated given the initial spatial distribution. The test calculates the mean nearest neighbor distances for dead and live trees where the null hypothesis takes the initial spatial distribution of the population as a given. The null distribution is created by shuffling the identity of living and dead trees 1000 times.

Meteorological data (NOAA 2002) were obtained for Liberty, Texas, 56 km west of the study site. This station provided the longest temporal record within a reasonable distance. Less-extensive records from the Beaumont Research Station, 16 km from the study site, were also examined; they indicated similar weather patterns. Mean temperature of the warmest month was calculated by averaging the daily minimum and the daily maximum for the summer months and then averaging the daily averages to get monthly means. The century average for the August mean temperature was also calculated. To calculate the mean temperature of the coldest month, this same procedure was repeated for the month of January. Night-time temperature of the coldest month was approximated by averaging the daily minimum temperatures in the month of January. An annual moisture index (annual precipitation/potential evapotranspiration; Box et al. 1993) was calculated. Potential evapotranspiration for Wier Woods was obtained from Caird (1996). Average precipitation of the driest month was calculated by summing daily precipitation per month, calculating the century average for each month, and then choosing the driest month.

For the age distributions of American Beech individuals at Wier Woods, data were used from 136 tree cores extracted from a random sample of the tree population as reported by Glitzenstein (1984; Glitzenstein et al. 1986).

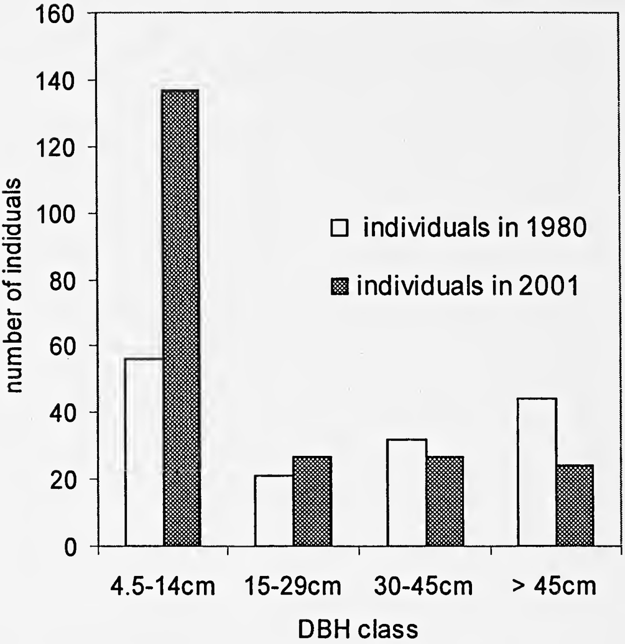

Fig. 2. Number of individuals in 1980 and 2001 by DBH class.

RESULTS

Population trends.—The original population of American beech trees tagged in 1980 consisted of 153 individuals > 4.5 cm DBH. Basal area of beech was 4.0 m^2/ha, 11.5% of stand basal area. By 2001, basal area of beech had declined to 2.7 m^2/ha in spite of an overall increase in stand basal area from 34.7 to 36.4 m^2/ha. The decline was strongly concentrated in the largest trees; the number of individuals ≥ 30 cm dropped and the number of smaller individuals rose between 1980 and 2001 (Fig. 2). The ≥ 45 DBH class experienced mortality at a rate of 4.10%/year, more than double the rate for the smaller size classes (Table 1). Mortality of largest trees was consistently higher than that of the whole population across the 20-year study period (Fig. 3). The step-function mortality model was significantly better in predicting large tree mortality than was the model assuming a constant probability of mortality over time (AIC of 257 vs. 267); the best step function was the one in which the increase occurred in 1986.

Average tree growth rates were variable. Dying large trees did not show significantly lower growth before mortality than surviving large trees ($F_{1,166}$ =.50, P=0.48).

Hurricane.—Beech mortality was high in 1987, the survey after the storm. Nevertheless, this was not the highest yearly mortality rate

Table 1. Percent mortality of American beech by size class six years before Hurricane Bonnie (1981-1986), one year after the hurricane (1987), six years after the hurricane (1987-92), the average across the study period (1981-2001), and the maximum annual rate.

Size Class (cm DBH)	Six Years Before	One Year After	Six Years After	Average	Highest
4.5 - 14	0.90	0.00	0.97	1.13	4.08 (1996)
15 - 30	0.00	0.00	1.85	1.55	10.00 (1992)
30 - 45	0.52	6.90	1.67	1.70	14.81 (1995)
>45cm	1.16	7.80	5.92	4.10	13.89 (1990)
total	0.77	3.52	2.50	2.03	5.11 (1990)

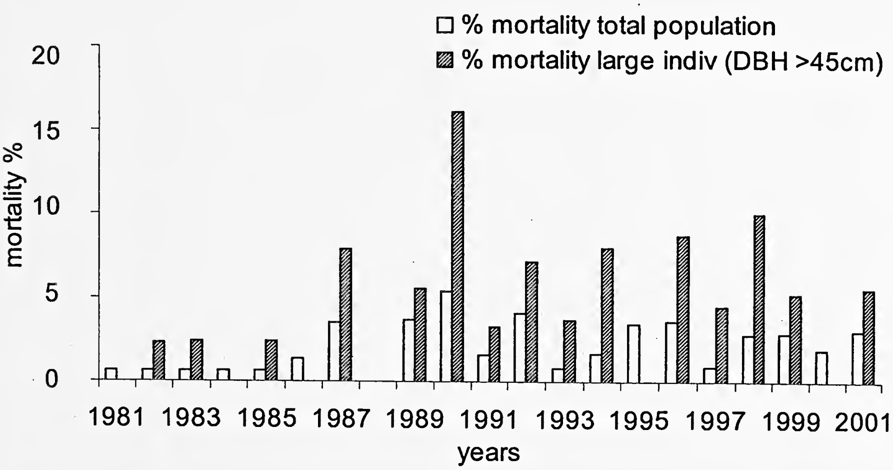

Fig. 3. Percent mortality of total beech population (dark bars) and large individuals of beech (light bars).

across the long-term study (Fig. 3, Table 1). Rather, Wier Woods lost most of its large trees gradually between 1987 and 2001. Mortality in the storm interval itself was not significantly different from the six years before the storm (χ^2 test; *df*= 1, *P*=.282); however, mortality was significantly greater after the storm than before for both the six-yr interval (χ^2 test, *df*= 1, *P*<.001) and the entire post-hurricane interval (χ^2 test, *df*= 1, *P*=.031). Logistic regressions of mortality *versus* DBH show the same pattern, i.e., that there was a significantly higher probability of mortality after the storm interval than before (for both the six-year and 15-year intervals) but not between the pre-storm interval and the storm interval itself (Fig. 4).

Climate.—After 1972, minimum temperature in August for Liberty, Texas rose steadily through 2001. In fact, 21 of last 23 summers exceeded the century average for minimum summer temperature, while precipitation showed no trends (Fig. 5). Wier Woods was above the

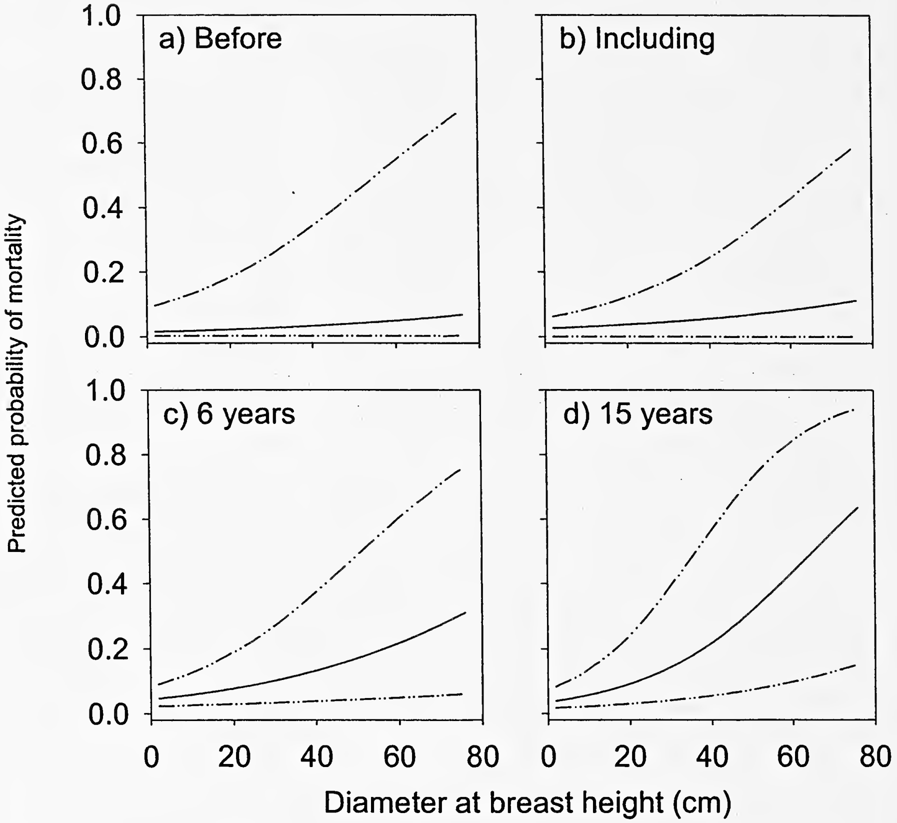

Fig. 4. Logistic regression curves of probability of mortality of American beech as a function of DBH for (a) six years before Hurricane Bonnie (1981-1986) (b) the census year including the hurricane (1987), (c) the six years after the hurricane (1987-92), and (d) the 15 years after the hurricane (1987-2001). Dashed lines represent 95% confidence intervals.

climate envelope of American beech for mean temperature of the warmest month (34° vs 29°C) but did not go below the bottom of the envelope for mean minimum temperature in the coldest month (15° vs 9°C). The annual moisture index (precipitation/potential evapotranspiration), was slightly below the minimum threshold (1.0 vs 1.1). Mean precipitation of the driest month was above the minimum threshold (88 vs 40 mm).

Pathogens/pests.—Dying trees had thin canopies and exhibited substantial leaf yellowing. Otherwise, none of the dying beech trees exhibited physical characteristics that might suggest death was caused by pathogens or parasites.

Spatial aggregation analysis showed that in 1980 living American beech trees of all sizes were uniformly distributed ($R = 1.11$, $P < .01$)

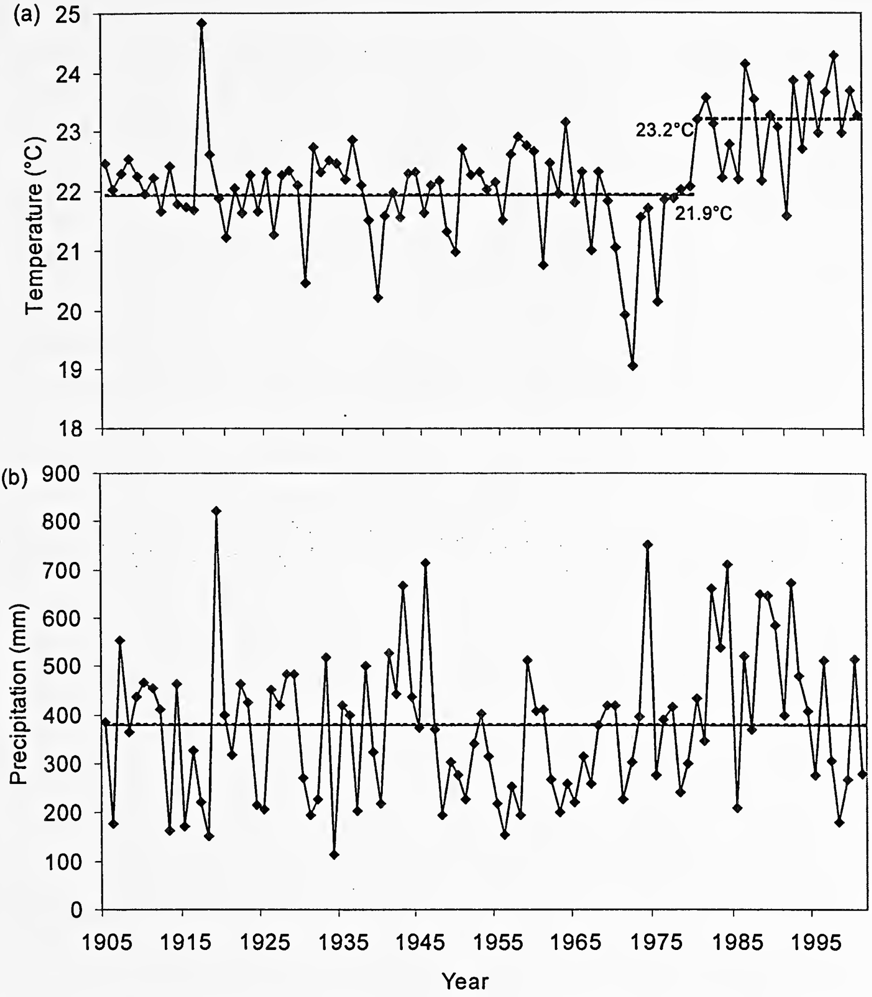

Fig. 5. Meteorological data from Liberty, Texas. (a) Minimum August temperatures. Dashed lines represent average minima for 1906-1980 (21.9°C) and for 1981-2002 (23.2°C). (b) Summer (May, June, July) precipitation. The solid line represents average summer precipitation for 1905-2002.

according to the Clark Evans nearest neighbor test. Large individuals were also uniformly distributed ($R = 1.27$, $P < .01$). Large trees dying between 1980 and 2001 were significantly aggregated ($R = .65$, $P < .01$), causing large living trees in 2001 to be randomly distributed. The randomization test confirmed that mortality was significantly aggregated ($P < .05$), even considering the initial distribution of the population.

Synchronous death.—The age distribution (Fig. 6) shows that beech trees have been germinating steadily since 1850, except for peaks in

1820-1870 and 1910-1950. Minima in ring widths in the 1920s and 1950s suggest that the population experienced two important periods of marked environmental change, the pine logging of 1917 and the drought of 1950 (Glitzenstein, et al. 1986). The drought of the 1950s was indeed the longest and worst in the state's climate history registering "severe" on the Palmer Drought Severity Index (NOAA 2003).

DISCUSSION

Beech mortality was clearly not randomly distributed in time or space, nor was the population even-aged, and so the decline is neither a consequence of a random fluctuation in large-tree mortality nor a result of synchronous death of an even-aged population; there was a significant decline beginning in 1987 in an all-aged population. To explain this decline, predisposing stress, pest/pathogen, and hurricane disturbance are considered independently, and then a combination of these causes is proposed.

Stress.—Stress due to drought is one of the most common factors that predispose populations to respond negatively to environmental stresses in the future (Pederson 1998). However, the 1950s drought occurred many years ago and so it is hard to imagine it had a major effect (but see Pederson 1998). A more immediate stress is the summer temperatures that are outside the climate envelope of beech, as defined by Box et al. (1993), recalling the high sensitivity of beech ring widths to August temperature (Cook et al. 2001). Large trees may be especially prone to temperature-related stress because of their greater exposure to sunlight and higher respiration.

Further support for climate stress is provided by recent range limit studies for American beech. For example, Iverson & Prasad (1998) predicted current distribution of American beech to be north of its actual distribution range, and Davis & Zabinski (1992) predicted that the American beech population would shift north if temperatures increased. The proximity of Wier Woods to the southwestern range limit of beech (Fig. 1) is relevant in this context since the influence of changing temperature would logically be expected to appear here first.

Pathogens/pests.—Two influences, aphid infestation (Siemann & Rogers 2003) and *Hypoxylon* (Pase 2002), have been documented on American beech in east Texas. However, neither aphids nor patches of their 'honey dew' secretions, were noted to be particularly abundant in Wier Woods during annual mortality surveys. Also, aphid feeding has minimal impact on large mature trees, causing its greatest damage and

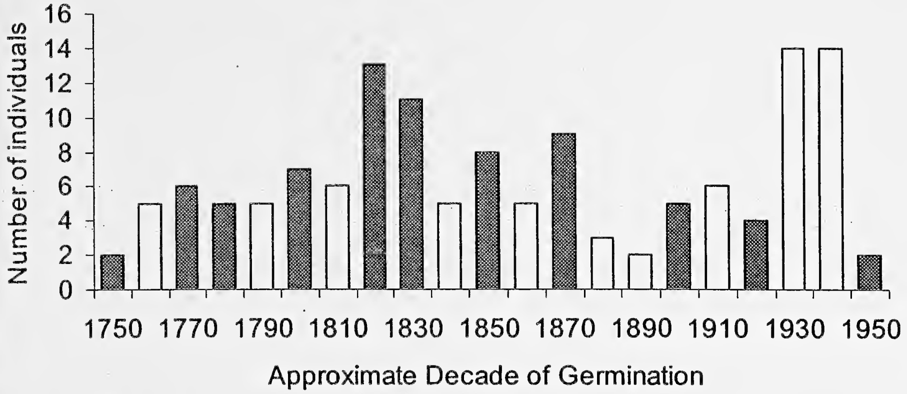

Fig. 6. The age distribution of a random sample of the beech population at Wier Woods based on ring counts from increment cores gathered by Glitzenstein (1986).

dieback in small trees less than 3 meters tall (Hemmingsen 2002).

Hypoxylon-infected water oaks are common, but *Hypoxylon* fungal cankers were observed on only a single beech tree in Wier Woods in a special inspection conducted in May 2003. Furthermore, patterns in growth rates at Wier Woods do not support the hypothesis that a fungal pathogen is causing beech decline. At Wier Woods, growth rates of dying large trees were not lower than those for living large trees, as might have been expected (see Houston 1979). However, it should be noted that the sample size for growth rates was small, and growth rate trends may be unclear given a small sample size and the inherently low growth rates of large, old trees.

Although there is little direct evidence for an effect of *Hypoxylon*, the aggregated mortality of large beech trees is consistent with the influence of a pathogen (but see below). A pathogen might also explain the extended duration of high mortality at Wier Woods, since pathogens may take months or years to affect their host (Hepting 1971), rather than causing mortality in one short time period. Given the high susceptibility of American beech to pathogens, the wide variety of pathogens known to affect beech, and the difficulty in documenting pathogen influences, this possible cause cannot be completely ruled out.

Hurricane.—In a mesic forest in northern Florida, after a hurricane more severe than Hurricane Bonnie, Batista et al. (1998) found that large American beech trees experienced moderate direct hurricane mortality (8.2%) and low overall post-hurricane mortality (Batista & Platt 2003). Assuming that a more intense storm would cause greater immediate damage to large American beech trees (Batista et al. 1998, Batista & Platt 2003), the lower immediate mortality and higher post-hurricane mortality in Wier Woods suggests that Hurricane Bonnie was not intense enough to account for the decline of the beech population. Furthermore, although the hurricane could have resulted in delayed mortality (cf., Putz & Brokaw 1989), mortality has remained high for more than 15 years after the hurricane, which suggests that other factors are influencing population mortality.

Synthesis.—Tree population declines occasionally may be the result of a single environmental factor, but they most often have multiple causes (Manion 1981). Some of these are predisposing factors, occurring months or even years, before tree mortality, and others are inciting factors precipitating an episode of mortality (Houston 1987). The hurricane could have been such an inciting factor. By damaging trees, it might have triggered an increase in mortality (Putz & Brokaw 1989) in a population already weakened by a predisposing factor such as the consistently increasing summer temperatures in the 1980s and 1990s. Pathogens often appear on host species after periods of climate stress, and trees weakened by climate stresses (Houston 1987) or hurricane injury (Putz & Brokaw 1989) can be especially susceptible to attacks of insects or fungi. Hurricane damage to the crowns of large beech trees could also increase heat loading on remaining nearby trees and could therefore explain the spatial aggregation of mortality.

Thus stress due to high summer temperatures, in conjunction with hurricane disturbance and possible pathogen influence, provides the most consistent hypothesis to explain the observed decline in American beech at Wier Woods. Further empirical observation of this beech population, as well as surveys of other beech populations in southeast Texas, will be required to fully evaluate this hypothesis.

ACKNOWLEDGMENTS

We thank Saara DeWalt and Jie Lin for their advice on statistics and SAS; the Wier family and the Nature Conservancy for permission to work in Wier Woods; and Peter Marks (Cornell University) David Appel (Texas A&M University) and Elgene Box (University of Georgia) who shared their thoughts and research results with us.

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COMPARATIVE ANALYSIS OF GROWTH AND MORTALITY AMONG SAPLINGS IN A DRY OAK-PINE FOREST IN SOUTHEAST TEXAS

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Abstract.—The role of shade tolerance in the dynamics of a sandy upland pine-oak forest in Big Thicket National Preserve, southeast Texas was investigated. Using a forest dynamics modeling framework, radial growth of saplings as a function of light availability and mortality as a function of recent growth history for species with a range of shade tolerance levels was investigated. In low light, shade-tolerant species grew faster than shade-intolerant species. However, in high light, shade-intolerant species did not grow faster than shade-tolerant species possibly because some of them are adapted for drought resistance. They did not survive better, either, perhaps because of recent increases in canopy shading. Mesic, shade-tolerant species had better performance at the dry site than at the mesic site, possibly because of a difference in the competitive environment of the two sites. An implication of invasion and higher growth and survival of the mesic species is that these species may have been limited to a larger extent by fire than by site conditions on this site in the past.

Broad patterns in species dominance across the landscape are well known for the southeastern United States (Christensen 1988; Ware et al. 1993), and these are consistent with general understanding of physiological tolerances of the major tree species. In southeast Texas, interspecific differences in response to light are consistent with trends in species dominance at a mesic site (Lin et al 2001; 2002), and thereby help provide mechanistic underpinning for observed species dominance on mesic sites. At a wet site, light was important in helping to explain species dominance, but only if response to flooding was considered, as well (Hall 1993; Hall & Harcombe 1998; 2001; Lin et al. 2004). In the study reported here, analysis of the light response to a dry site is extended, partly to further investigate the effects of site differences on light responses, and partly also to determine whether differences in light response among species help explain changes in species dominance.

The approach is based on the general understanding that light, soil moisture and nutrients are important factors that determine species composition of many terrestrial plant communities (e.g. Huston & Smith 1987; Smith & Huston 1989; Pacala et al. 1994; Knox et al. 1995; Sipe & Bazzaz 1995; Grubb et al. 1996; Catvosky & Bazzaz 2000). Mortality-growth-light relationships based on the forest dynamics model, SORTIE (Pacala et al. 1993; 1994; 1996; Kobe et al. 1995) are used. The model assumes resource competition among coexisting species, as do most forest dynamics models (e.g. Botkin et al. 1972; Shugart 1984; Smith & Huston 1989; Pacala et al. 1996). Through repeated iterations of the model, light competition results in shifting dominance from shade-intolerant species to shade-tolerant species over the course of stand development. Extending SORTIE by incorporating soil moisture into the mortality-growth model, Caspersen & Kobe (2001) found that species ranks in mortality-growth relationship shifted substantially across soil moisture gradient, resulting in shifting dominance.

Although competition for soil moisture provides a possible process-level explanation for the broad pattern of species segregation across the landscape in southeast Texas (Marks & Harcombe 1981; Harcombe et al. 1993) and across the southeastern United States (Christensen 1988; Ware et al. 1993), fire also plays a role (Harcombe et al. 1993; 1998). Under the fire scenario, sites with longleaf pine (*Pinus palustris*), a species highly tolerant to fire, would not support mature hardwood forests. One way to investigate the question of the relative importance of soil moisture and fire is to compare growth-mortality relationships of species under different moisture regimes. In essence, this is asking whether consistency can be found between process (growth/mortality) and pattern, and tie it to a mechanism (competition for light and/or mois-ture). If growth and mortality for species present at different sites are lower at the dry site, the inference that soil controls vegetation pattern cannot be ruled out. If, on the other hand, growth and mortality are higher at the dry site under the current fire suppression scenario, then fire may have been the major limiting factor at the dry site in the past.

In this study, light competition in a mixed pine-oak stand in the Turkey Creek Unit of the Big Thicket National Preserve, southeast Texas was investigated. In addition, growth and mortality of species common to both this dry site and a nearby mesic site were compared. Compared with the mesic site, the dry site is characterized by coarser soils and lower soil moisture availability (Caird 1996). Widespread presence of charcoal on stumps and the prevalence of longleaf pine indicates that the dry site probably burned relatively frequently (Harcombe et al. 1993). Under the current fire suppression scenario, the site is being invaded by mesic species (Harcombe et al. 1998). The invasion of mesic species suggests that they may have been limited by fire in the past, and not by low soil moisture. The following questions are addressed: Do differences in mortality-growth-light relationship among species within and between sites explain differences in dominance between the dry site and the mesic site? Can species responses to site conditions explain differences in species composition or must historical disturbances (e.g., fire) be invoked?

STUDY SITES AND SPECIES

The dry study site is located on a low, sandy ridge in the Turkey Creek Unit of the Big Thicket National Preserve about 10 km southeast of Warren, Tyler County, Texas (30°35'N, 94°24'W). The climate of the area is humid subtropical with an annual rainfall around 1475 mm. The soil is a sandy loam of Landman series, loamy, siliceous thermic Grossarenic Paleudalf (Caird 1996). Light measurements obtained from hemispherical photos taken at plot centers (100 plots in total) indicated a light range in the understory from 1.7% full sun to 33.5% full sun with a mean of 12.8%.

The vegetation is dominated by oaks and pines. Ranked in decreasing order of relative abundance, post oak (*Quercus stellata* Wang.), southern red oak (*Quercus falcata* Michx.), black hickory (*Carya texana* Buckl.), longleaf pine (*Pinus palustris* Mill.), loblolly pine (*Pinus Taeda* L.) and shortleaf pine (*Pinus echinata* Mill.) form a relatively open canopy 15-20 m tall. Basal area increased from 21m^2/ha in 1982 to 28 m^2/ha by 1999. Red maple (*Acer rubrum* L.) and sweetgum (*Liquidambar styraciflua* L.) are minor canopy components. The understory is a moderately dense mixture of tree saplings and shrubs; flowering dogwood (*Cornus florida* L.), yaupon (*Ilex vomitoria* Ait.) are abundant. Saplings of mesic species, such as Southern magnolia (*Magnolia grandiflora* L.) and American holly (*Ilex opaca* Ait.) have become more abundant since 1980 (Harcombe et al. 1998). American holly and flowering dogwood are very shade-tolerant; sweetgum and most dry-site species are shade-intolerant. The above shade tolerance categories are based on conventional wisdom regarding shade tolerance as summarized by Burns & Honkala (1990). These shade tolerance classifications are based largely on field observations regarding the relative abundance of different species in the forest understory.

Table 1. Latin names, common names, name codes and shade tolerance of major species. Species are arranged in ascending order of shade tolerance according to Burns & Honkala (1990).

Latin Name	Common Name	Species Code	Shade Tolerance	Site Affiliation
Quercus stellata	Post oak	QUST	Intolerant	Dry
Carya texana	Black hickory	CATE	Intolerant	Dry
Pinus palustris	Longleaf pine	PIPA	Intolerant	Dry
Pinus echinata	Shortleaf pine	PIEC	Intolerant	Dry
Pinus Taeda	Loblolly pine	PITA	Intolerant	Mesic, dry
Liquidambar styraciflua	Sweetgum	LIST	Intolerant	Mesic, dry
Quercus falcata	Southern red oak	QUFA	Intermediate	Dry
Acer rubrum	Red maple	ACRU	Tolerant	Mesic, dry
Magnolia grandiflora	Southern magnolia	MAGR	Tolerant	Mesic, dry
Ilex opaca	American holly	ILOP	Very tolerant	Mesic dry
Cornus florida	Flowering dogwood	COFL	Very tolerant	Mesic, dry

The dry site was logged in 1930 but the stand is not strongly even-aged (Harcombe et al. 1993; Kaiser 1995); apparently many old hardwoods and older pines were left in the site. Exactly how long ago fire occurred on this site is unknown. The presence of charcoal on stumps implies relatively frequent fire prior to 1930 and relatively infrequently after that until 1974. Fire has been absent since 1974 (Kaiser 1995; P. Harcombe, personal communication).

A nearby mesic site was chosen for comparison. The mesic site is located in Hardin County, Texas (30°16'N, 94°12'W) approximately 14 km away from the dry site. Species composition of this site represents many typical mesic sites throughout the Coastal Plain area of the southeastern U.S. (Marks & Harcombe 1981). The site is dominated by loblolly pine (*Pinus taeda* L.), water oak (*Quercus nigra* L.), white oak (*Quercus alba* L.), American beech (*Fagus grandifolia* Ehrh.) and southern magnolia (*Magnolia grandiflora* L.). Red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.) and sweetgum (*Liquidambar styraciflua* L.) are abundant as small to medium stems but are infrequent as large trees. Important understory trees include American holly (*Ilex opaca* Ait.) and flowering dogwood (*Cornus florida* L.). Basal area has varied between 33.7 m^2/ha (after hurricane) and 35.1 m^2/ha over the last 20 years. More detailed description can be found in Glizenstein et al. (1986) and Lin et al. (2001; 2002). See Table 1 for shade tolerances and affiliations of species with sites.

DATA COLLECTION AND ANALYSES

Sapling growth.—The dry study site is 4 ha divided into 100 contiguous tree plots. Each plot is 20m by 20m. Tree surveys were performed in 1980, 1982, 1985, 1989, 1994, 1997 and 2000. During tree surveys, stems with a Diameter at Breath Height (DBH) ≥ 2 cm are measured with a diameter tape. A subset of 16 plots was chosen randomly for annual measurement of saplings (height ≥ 140 cm and DBH ≤ 4.5 cm), in which DBH of all saplings was measured to the nearest 0.1 cm from 1980-2000. All trees and saplings are tagged with an identification number. For each sapling (height ≥ 140 cm and DBH ≤ 4.5 cm), annual radial growth rate over three years was calculated as the difference in radius between year 1999 and year 1996 divided by 3. The average over 3 years was used to reduce measurement variation. Calculations of growth were made for all species with more than 15 individuals in the sample.

As approximations of high-light growth and low-light growth, top quartile growth rate (TQGR) and bottom quartile growth rate (BQGR) were calculated. Approximations were chosen because it was not possible to model mortality-growth-light relationships owing to small sample sizes and/or insufficient range of light conditions, TQGR is a reasonable approximation of high-light growth because saplings that have high growth rates are unlikely to be growing in low light. Comparison of TQGR and the actual high-light growth in the mesic site where both measures are available showed a good agreement between the two (data not shown). It is important to note that bottom quartile growth rate is only a rough approximation of low-light growth because low growth could result from many reasons other than low light.

Top quartile growth rate was computed as follows: First, the radial growth rate over the first 3 years after the sapling first entered the survey was calculated. After calculating growth rates of all first-year saplings, growth rates were sorted in descending order. Then saplings with growth rates in the top 25% were chosed and their growth rates were averaged. To see whether TQGR of first-year sapling obtained this way might underestimate maximum growth, it was compared with TQGR for all saplings present in one period (1996-1999); it did not (results not shown). The bottom quartile growth rates were obtained by taking the bottom 25% growth rates and computing the average.

Light measurement.—A subset of live saplings was selected from the database for light measurements. In keeping with the protocols of previous studies, the goal was to find at least 50 saplings per species for light measurement. The final sample size ranged from 45 to 59 saplings per species. The six species are: red maple, sweetgum, loblolly pine, post oak, Southern magnolia and American holly. Saplings were selected in a stratified random fashion by plot to obtain a broad range of light conditions. Fish-eye photographs were taken at the top of each sapling (following Rich 1989; Pacala et al. 1994) in mid summer (late June to mid July), 1999. To increase contrast, all photos were taken early in the morning before sunrise and late in the afternoon after sunset when skylight is evenly distributed. Moreover, all photos were taken on Kodak TMAX ASA 400 (black and white) film and the film was underexposed by 1 f-stop to further enhance contrast. The images were scanned, digitized and analyzed using CANOPY (Rich 1989). Threshold values were set individually to minimize the "halo effects" (Anderson 1964). The global site factor (GSF) was estimated from each photo. GSF is an estimation of the fraction of total radiation (both diffuse and direct) a sapling experienced during the growing season. The GSF value was converted to percent of full sun by multiplying GSF by 100. Since no major canopy disturbances occurred during the 1996-1999 period, the light level captured in 1999 was considered to be a reasonable representation of average light environment over the three-year period at a given location.

Sapling mortality.—In addition to periodic measurement, each sapling was checked annually to see whether it was dead or alive. Survival time was calculated as the length of time a sapling was followed during the course of the study. If a sapling died, then its survival time would be the difference between the year of death and the year it entered the study. If a sapling was alive at the end of the study (Year 1999), its survival time was the difference between the ending year and the year it entered the study. Saplings that were alive at the end of the study were flagged as right censored (Cox & Oakes 1984; Lee 1992). All saplings (dead or alive) that had been recorded since the beginning of the long-term study (Year 1980) were included. To model mortality as a function of recent growth, pre-mortality growth rate was calculated for dead saplings as the difference in radius over the last 3 years prior to death divided by 3.

Growth-light analysis.—The goal of this analysis is to model growth response from light availability using a Michaelis-Menten function, as in previous studies (cf. Pacala et al. 1994; Wright et al. 1998). However, because of sampling limitations, the asymptote parameter was replaced by TQGR, which is treated as a constant instead of a parameter, because of inadequate range of conditions and small sample sizes for some species. The one-parameter model takes the following form:

$$\mu = \frac{aL}{a/S + L} \tag{1}$$

Where μ is the mean growth response given light availability; a is the TQGR; S is the slope at low light; L is the light availability (% of full sun).

The maximum likelihood methods to estimate parameter S was used. The final likelihood function is:

$$\prod_{i=1}^{n}[\frac{1}{\sqrt{2\pi C[aL/(a/S+L)]^{D}}} - \exp(-\frac{[Gi - aL/(a/S+L)]^{2}}{2C[aL/(a/S+L)]^{D}})] \tag{2}$$

where G_i is the radial growth rate of sapling i (3-year average); C, D are two parameters that account for heteroscedasticity.

Confidence intervals of S were obtained by bootstrapping. Both model fitting and bootstrapping were done using Splus 6.0 on Unix (Mathsoft, Inc. 2000). A more detailed description of the maximum likelihood estimation method can be found in Lin et al. (2002).

Mortality risk (annual death rate) as a function of growth.—Survival analysis was used to model mortality risk as a function of growth. The likelihood function for censored and non-censored saplings is (Lee 1992):

$$\prod_{i=1}^{r} \lambda e^{-\lambda T_i} \prod_{i=1}^{n-r} e^{-\lambda t_i} \tag{3}$$

where r is the number of saplings that died during the study and n-r is the number of saplings that are right-censored. T_i and t_i are lifetimes of a non-censored and right-censored sapling i, respectively; λ is the parameter of mortality risk (annual mortality risk).

A negative exponential function was used to estimate λ from predictor variables

$$\lambda = e^{-\beta_0 - \beta_1 X_1 - \beta_2 X_2} \times \theta \tag{4}$$

where X_1 is the radial growth rate (mm/yr); X_2 is the initial size (radius in mm). The parameters to be estimated are the ßs. θ is the error term. Estimates of parameters β_0, β_1 and β_2 were found by maximizing the likelihood function (3).

Maximum likelihood estimation of annual death rate.—To further explore how mortality might be different among species with different shade tolerance, annual death rate was also compared.

The maximum likelihood estimator of annual death rate is (Lee 1992):

$$\hat{\lambda} = \frac{D}{\sum_{i=1}^{D} T_i + \sum_{i=1}^{N-D} t_i} \tag{5}$$

Where D is the number of deaths during the time interval.

The 95% confidence interval of λ is:

$$\hat{\lambda} \pm \frac{\hat{\lambda} \times 1.96}{\sqrt{D-1}} \tag{6}$$

RESULTS

Growth response to light and inter-specific tradeoff.—Growth increased with light for all species (Figure 1). Except for sweetgum, which showed higher growth than red maple, the pattern of low-light growth was consistent with the expectation that shade-tolerant species grow faster in low light than shade-intolerant species (Figure 1). The low-light growth index, slope at low light, was highest for American holly, followed by southern magnolia (Table 2). Two shade-intolerant species, loblolly pine and post oak, ranked low in slope (Table 2). The correspondence between low-light growth and shade tolerance ranks was further supported by the comparison of bottom quartile growth rates among species (Figure 2a): Shade-tolerant species ranked higher than most shade-intolerant species in bottom quartile growth rates, though bottom quartile growth rate of sweetgum and loblolly pine were higher than expected based on standard shade tolerance ranks.

In contrast, for high-light growth, the order of TQGR did not correspond to shade tolerance expectation: First, shade-intolerant post oak and loblolly pine showed low TQGR; second, shade-tolerant southern magnolia and American holly grew more rapidly than expected (Figure 1, Table 2). Top quartile growth rates of xeric dominants (e.g., post

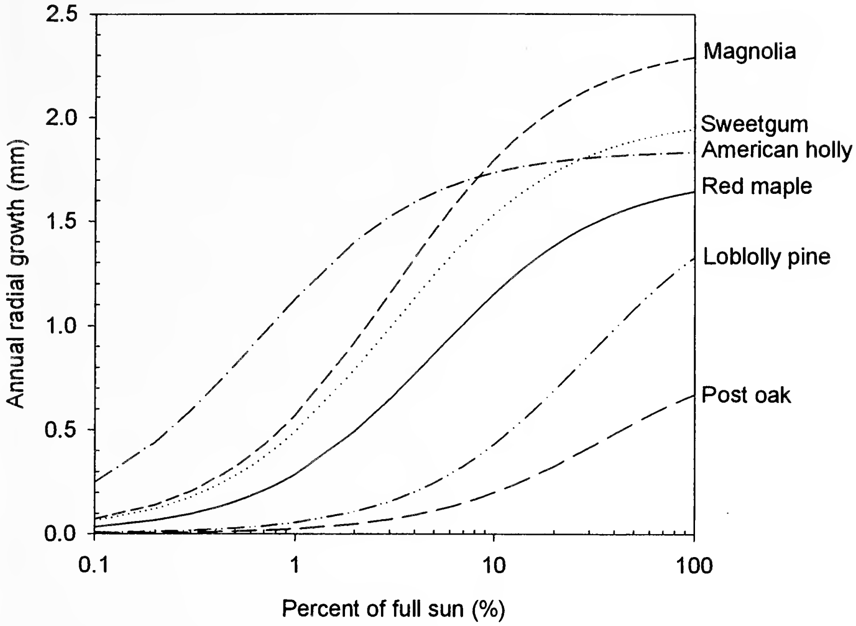
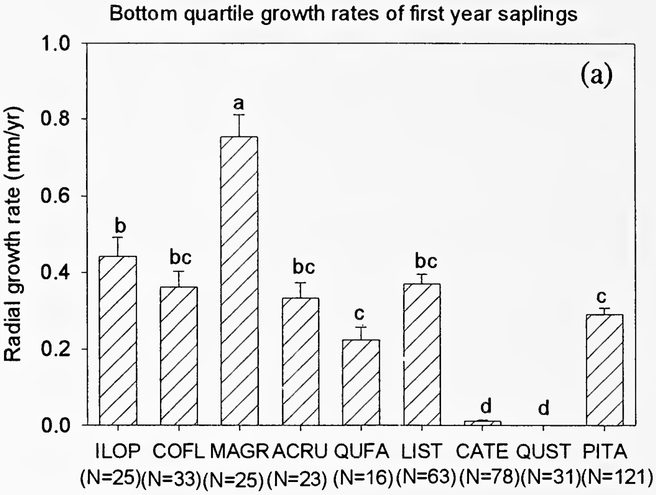


Fig. 1. Fitted growth-light regression curves for different species using equation (1). The horizontal axis represents percent of full sun (log scale); the vertical axis represents annual radial growth.

Table 2. Top quartile growth rates (TQGR, a in equation 2) and estimated slope at low light (S in equation 2) with 95% confidence intervals (CI). *N* is the sample size. NA stands for not available.

Species	Shade tolerance	N	TQGR	CI of TQGR	S	CI of S
Post oak	intolerant	53	0.905	0.736-1.074	0.026	0.014-0.046
Black hickory	intolerant	78	0.718	0.641-0.795	NA	NA
Loblolly pine	Intolerant	59	1.720	1.643-1.798	0.058	0.033-0.099
Sweetgum	Intolerant	58	2.006	1.912-2.099	0.654	0.357-1.100
Southern red oak	Intolerant	16	1.263	1.155-1.370	NA	NA
Red maple	Tolerant	45	1.728	1.599-1.857	0.347	0.232-0.530
Southern magnolia	Tolerant	52	2.363	2.205-2.516	0.755	0.545-1.123
American holly	Very tolerant	47	1.847	0.901-1.282	2.911	1.650-5.144
Flowering dogwood	Very tolerant	33	1.944	1.831-2.057	NA	NA


Bottom quartile growth rates of first year saplings

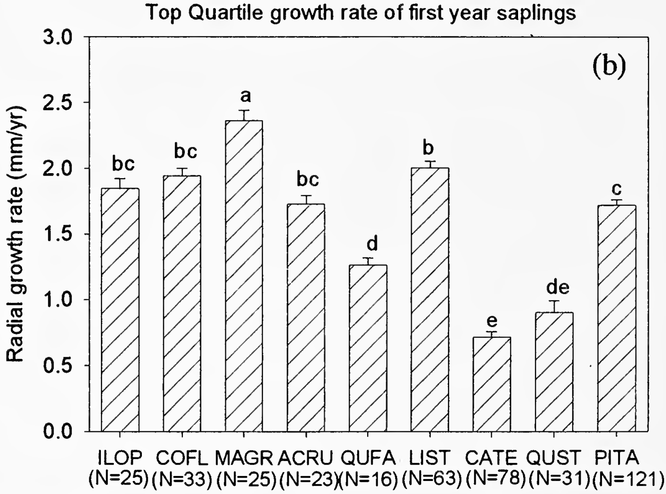

Top Quartile growth rate of first year saplings

Fig. 2. Bottom quartile growth rates for different species (a) and top quartile growth rates for different species (b). Values not sharing the same letter are significantly different (*ANOVA* followed by Tukey's multiple comparison adjustment, $P < 0.05$). N is the number of saplings. Species are arranged in descending order of shade tolerance from left to right. See Table 1 for key to species codes.

oak, black hickory, southern red oak) were significantly lower ($P < 0.05$; *ANOVA* followed by Tukey's multiple comparison adjustment) than mesic invaders (e.g., American holly, Southern magnolia, sweetgum). Even within the six mesic species, top quartile growth rates did not conform to expectation: shade-tolerant southern magnolia grew significantly faster than shade-intolerant sweetgum and loblolly pine (Figure 2b).

Mortality risk as a function of growth.—Mortality risk as a function of growth was used to characterize shade tolerance in previous studies (e.g., Kobe et al. 1995; Lin et al. 2001). In this study, the low number of dead saplings of American holly, southern magnolia and red maple made survival analysis on these species unreliable (e.g., there was only one dead American holly sapling and two dead southern magnolia saplings found in the long-term study data base). Thus, at this site, the only shade-tolerant species included in survival analysis was flowering dogwood. In contrast to results of a previous study performed at the mesic site (Lin et al. 2001), both growth and size were significant predictors of mortality risk in the dry site. Overall, mortality risk decreased as growth increased and decreased with increasing size (Table 3). The mortality-growth relationship was not consistent with the expectation that shade-intolerant species have higher mortality risk at zero growth and steeper slope than shade-tolerant species (Table 3).

Annual death rate.—Interpretation of the above mortality-growth responses in terms of shade tolerance expectation was limited by the fact that only one shade-tolerant species (dogwood) was involved in the analysis. Therefore, annual death rates among species were also compared (Figure 3). Mesic species such as American holly, southern magnolia, red maple exhibited extremely low annual death rate (Figure 3), which is consistent with the previous finding that they have become more abundant and species typical of dry sites have experienced dramatic decline (Harcombe et al. 1998). Death rates of dry site dominants (longleaf pine, post oak, southern red oak) were consistently higher than mesic site species.

Cross-site comparisons.—Growth-light curves of southern magnolia and American holly were significantly higher at the dry site than at the mesic site over the light range (Figure 4a and b): For red maple, growth rates were significantly higher only above 60% full sun (Figure 4c). For sweetgum, there was no significant difference between sites (confidence interval overlapped, not shown) (Figure 4d). Annual death rates were significantly higher at the mesic site than at the dry site for all species common to the two sites except flowering dogwood (Figure 5).

DISCUSSION

Growth, mortality and tolerance.—Results show that growth responses to low light are roughly consistent with one of the expectations regarding shade tolerance: in low light, shade-tolerant species grow faster than

Table 3. Parameter estimates of the mortality-growth model (equation 4) with 95% confidence intervals (CI) for different species. *N* is the total number of saplings (both dead and live); βs are parameters in equation 4. λ is the mortality risk at zero growth at size class 0.5 mm.

Species	Shade tolerance	Sample size (*n*)	β_0	β_1	β_2	CI of β_0	CI of β_1	CI of β_2	λ	CI of λ
Post oak	Intolerant	1563	2.15	1.46	0.03	1.93-2.37	0.87-2.05	0.02-0.04	0.11	0.09-0.14
Black hickory	Intolerant	441	3.50	0.28	0.06	2.89-4.10	-1.27-1.83	0.03-0.09	0.03	0.02-0.05
Longleaf pine	Intolerant	58	2.39	1.08	0.02	1.34-3.44	-0.32-2.48	-0.02-0.05	0.09	0.03-0.27
Shortleaf pine	Intolerant	133	2.21	1.71	0.04	1.62-2.80	0.40-3.02	0.02-0.07	0.11	0.06-0.20
Loblolly pine	Intolerant	1573	1.70	0.83	0.05	1.52-1.88	0.59-1.07	0.05-0.06	0.18	0.14-0.21
Sweetgum	Intolerant	264	2.85	3.44	0.03	2.17-3.54	1.73-5.15	0.00-0.06	0.06	0.03-0.11
Southern red oak	Intermediate	178	3.17	1.18	-0.01	2.59-3.75	0.25-2.10	-0.03-0.00	0.04	0.02-0.08
Flowering Dogwood	Very tolerant	291	2.29	0.46	0.02	1.99-2.58	0.14-0.78	0.00-0.03	0.10	0.07-0.14

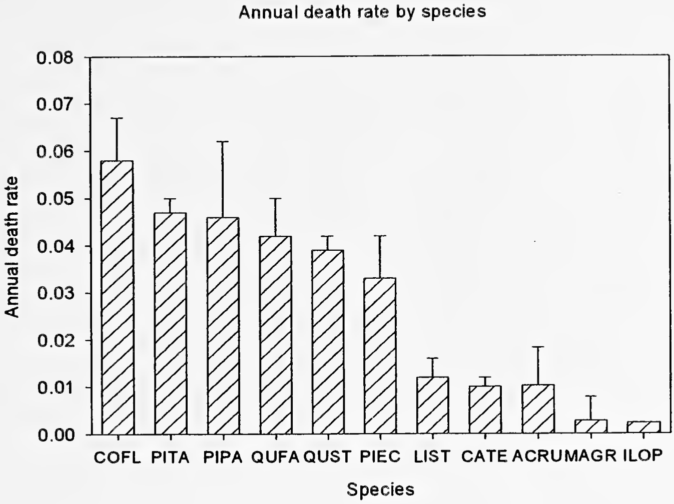


Fig. 3. Annual death rates for different species. Calculation is based on equations 5 and 6.

shade-intolerant species, even on dry sites. However, growth responses to high light do not correspond to the expected pattern. Instead, two shade-intolerant species, post oak and loblolly pine, have lower high-light growth than expected. Why loblolly pine showed lower high-light growth than expected remains an interesting question for further investigation. The low growth of post oak can possibly be explained by drought tolerance. The inherent conflict between carbon uptake and water loss of plant has been widely documented and intensively studied (e.g., Field & Mooney 1986; Huston & Smith 1987). Adapted to soil water deficiency, drought-tolerant species are reported to develop traits that minimize water loss but limit growth rates (Delucia et al. 1988; Kozlowski et al. 1991; Barton & Teeri 1993). Indeed, the three xeric dominants (post oak, black hickory and southern red oak) in this study ranked the lowest in both top quartile growth rates and bottom quartile growth rates (Figure 2) indicating slow growth of drought-tolerant species (Chapin 1991).

With respect to mortality, the positive association of initial size and survivorship has also been reported in other studies (e.g., Clark & Clark 1992; Condit et al. 1995; Sheil & May 1996; Kobe 1999). Compared with the mesic site (Lin et al. 2001), where a significant effect of size was not detected, saplings at the dry site span a wider size range, so the significant effect of size on mortality in this study may be attributable to

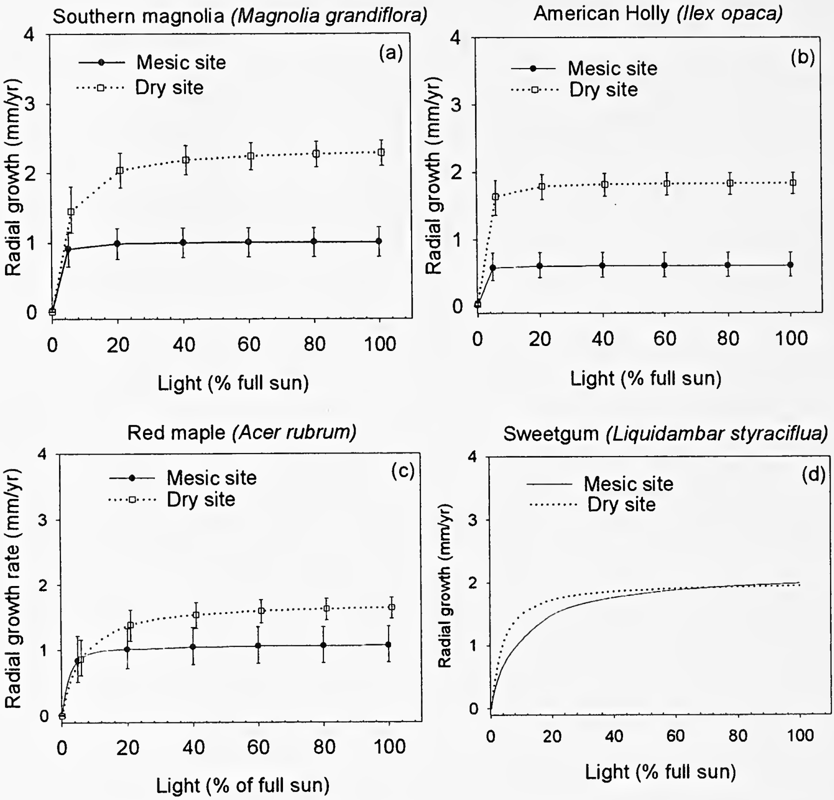


Fig. 4. Cross-site comparison of fitted radial growth (with 95% confidence interval) vs. light: (a) Southern magnolia; (b) American holly; (c) Red maple; (d) Sweetgum.

relatively large size variation (cf. Kobe 1999). In addition, the decline of mortality with size may be an indication that larger saplings with more extensive root systems suffer less drought-induced mortality on dry sites, as suggested by Caspersen & Kobe (2001).

The higher death rate for xeric species than most mesic species (Figure 3) can possibly be explained in terms of stand dynamics and change in light environment over the last 20 years. Stem density increased about 15% from the early 1980s to the 1990s, and most of the increase in total stem density was caused by increased density of understory dominants, such as yaupon (*Ilex vomitoria*), southern magnolia and American holly (Kaiser 1995). A direct consequence of an increase in density of understory species is reduced light penetration to the understory, which would cause the high death rates of shade-intolerant xeric dominants.

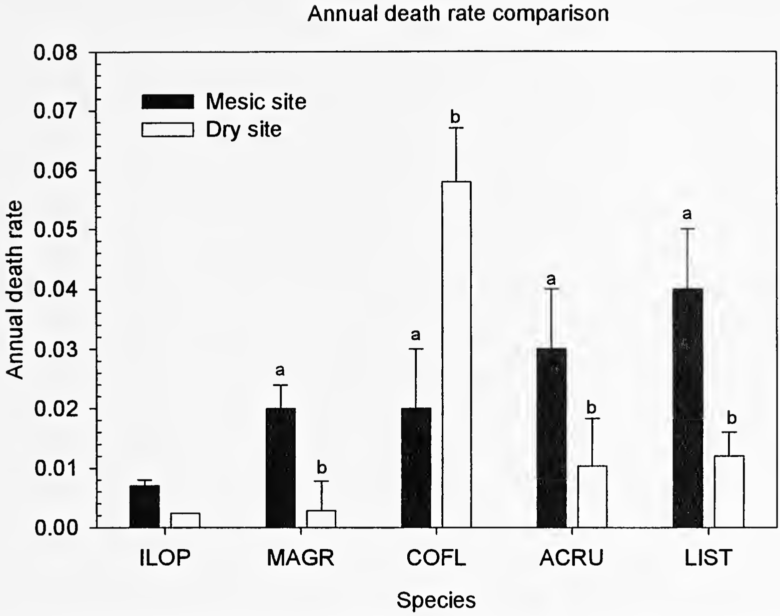


Fig. 5. Cross-site comparison of annual death rates. Values not sharing the same letter are significantly different between the two sites.

As an exception to the pattern of low death rate of shade-tolerant species, flowering dogwood had a higher death rate than even shade-intolerant species. This high mortality is consistent with a declining trend of this species over its range, which is associated with the exotic fungus, anthracnose (*Discula destructiva*) in the Great Smoky Mountains, but not elsewhere (Schrope 2001). It was noted that fire suppression, which results in thicker canopy and increased moisture, help the fungus to thrive (Schrope 2001).

Cross-site comparison and implications for stand dynamics.—Previous studies have shown that the combined effect of soil moisture and light on plant performance (growth and survivorship) may largely depend on the balance between the improvement allowed by one environmental factor (e.g., light) and the reduction imposed by deterioration in another factor (e.g., soil moisture) (Berkowitz et al. 1995; Holmgren et al. 1997). At drier sites, if the negative effects of soil moisture deficiency on plant performance do not outweigh the positive effects of more light penetration resulting from the more open canopy, then better performance at drier sites would be expected. In fact, many studies have reported such "facilitative" effects at drier sites (Parker & Muller 1982; Barton 1993; Belsky et al. 1993; Berkowitz et al. 1995; Kobe & Coates 1997). In an experiment testing the effects of community composition on growth and survival of tree seedlings, Berkowitz et al. (1995) noted that in sites that were physically unfavorable, surrounding vegetation had few negative effects (competition) on seedling growth. In the case of sugar maple in their study, surrounding vegetation actually facilitated growth of sugar maple seedlings. So growth performance was not only influenced by site suitability, but depended on surrounding vegetation, as well. This conclusion may provide an explanation for what was observed. For mesic species (magnolia, American holly and red maple) in this study, saplings at the dry site may benefit from less competition for soil resources from slow-growing neighboring vegetation, and thereby maintain a favorable growth and survival status, even though there is more total available water at the mesic site than at the dry site (Caird 1996). The exception, sweetgum, failed to exhibit higher growth at the dry site possibly because it is less drought-tolerant than others (Marks & Harcombe 1981) and therefore suffered more drought-induced growth reduction.

The better performance of shade-tolerant mesic species at the dry site is not consistent with the idea that there is trade-off between shade tolerance and drought tolerance (e.g., Smith & Huston 1989). Instead, these species appeared to be both shade-tolerant (i.e., grow faster and/or survive better in shade than shade-intolerant species) and drought-tolerant (i.e., better performance at dry site than at mesic site). It may be, however, that differences in drought tolerance only appear in years of more extreme drought or after saplings get large enough to be exposed to the drying effect of full sun. Alternatively, Caspersen et al. (1999) argued that whether species conform to a trade-off between shade tolerance and drought tolerance may depend on the relative importance of growth and survival in determining the species ability to tolerate limiting resources. If the ability to survive in the shade is achieved by allocation to defense and storage (Kitajima 1994; Kobe 1997), then tolerance to shade may also confer tolerance to other limiting resources, including soil moisture.

Pacala et al. (1996) argued that light competition can produce successional patterns in forest communities because of different light requirements of competing species. In a dry forest, light competition has its apparent signature in growth and mortality of saplings, although the correspondence between shade tolerance expectation and sapling performance is weaker than it is at moister sites. The better growth performance of shade-tolerant invaders in low light than shade-intolerant dominants, and the correspondence between the decline of shade-intolerant dominants and canopy closure clearly suggest that this forest is undergoing successional changes driven by light competition as suggested by Harcombe et al. (1998); i.e., mesic species do not seem to be limited by low soil moisture in this forest. Instead, they grow faster and survive better than at the moister site. While light competition may be a major driving force of dynamics in this forest, the fact that the light responses of some species (such as flowering dogwood and sweetgum) do not conform to the expected pattern of light competition points to the inadequacies of the SORTIE model. In fact, aside from shade tolerance, tradeoffs involved in drought tolerance, herbivore tolerance and fire tolerance may be of importance to explain the observed deviations.

Returning to the question regarding the extent to which the effects of site conditions and/or fire contribute to stand composition and dynamics, the data showed that saplings of mesic species have better performance at the dry site than at the mesic site in terms of both growth and survivorship. Thus, mesic species do not seem to be limited by site conditions under the current fire exclusion scenario. An important implication is that mesic species may have been limited to a larger extent by fire than by site conditions in the past (Harcombe et al. 1998), and that the effect of site conditionson vegetation pattern may be as much indirect via its effect on fire as it is direct via its effect on differential growth and mortality among species.

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STRUCTURAL CHANGES AFTER PRESCRIBED FIRE IN WOODY PLANT COMMUNITIES OF SOUTHEASTERN TEXAS

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Abstract.—A field experiment was conducted to study fire effects on woody plants in vegetation representing a gradient from dry to mesic types in southeastern Texas. There was little effect of fire on small sapling density or shrub cover, partly because post-fire recruitment of saplings by resprouting and germination was rapid. Fire caused declines in large saplings and small trees in most types, and in large trees in the drier vegetation types. That is, this study showed that fire effects varied according to vegetation type and stem size class; the effects were most pronounced for dry types and small trees. The effect of fire on stem density was lower in the mesic types probably because of differences in moisture, fuel characteristics, and species response.

Upland communities in the southeastern United States were mostly dominated by longleaf pine (*Pinus palustris* Mill.) in presettlement times (Wahlenberg 1946; Quarterman & Keever 1962; Harcombe et al. 1993; Ware et al. 1993; Schwartz 1994). Fire was the primary operational force in maintaining this vegetation pattern (Christensen 1988; Harcombe et al. 1993; Ware et al. 1993; Schwartz 1994). Logging, landscape fragmentation and fire suppression contributed to the decline of longleaf pine communities and expansion of other non-pyric communities. Prescribed fire has now been reintroduced in preserve lands across the region, and it is of interest to determine how this will affect the existing pattern which is a result of varying stand histories and varying site conditions. The interest derives from the observation that the response of vegetation may vary in different parts of the landscape (Christensen 1981; 1988; Romme & Knight 1981; Renkin & Despain 1992; Lertzman & Fall 1998; Breininger et al. 2002).

Some types of vegetation may change substantially if fire is applied because fires are hot or species are particularly susceptible. Other types may change little because of low fire intensity caused by specific attributes related to vegetation type, including fuel bed characteristics, soil moisture, and low susceptibility of species. While some of these factors will have countervailing effects, the general hypothesis is that mesic vegetation types will show less change than xeric types, primarily because of denser canopies, less-flammable hardwood litter, and higher soil moisture content (Marks & Harcombe 1981; Streng & Harcombe 1982; Liu et al. 1997). Higher available soil moisture (related to soil texture; Harcombe & Marks 1981) favors hardwood species which produce less-flammable foliage. This, in turn, results in tightly-packed fuel beds in which lower oxygen availability and higher moisture content cause fires to be cooler. Also, a site with higher available moisture can support a denser tree canopy, which can reduce the density of shrubs or ground-layer species capable of producing flammable fine fuels. Under these circumstances, even though the species on mesic sites may be more fire-sensitive, fires are cooler, so the mesic species persist.

Support was found for the hypothesis in a previous report on variation in species compositional change as a function of vegetation type (Liu et al. 1997). Although the differences were modest, vegetation types characteristic of dry sites in the Big Thicket of southeast Texas showed more compositional change than vegetation types characteristic of mesic sites. This followup study focuses on changes in structural attributes of the vegetation (shrub cover, density of saplings and trees). This provides additional information on the magnitude of the differential response, and it does so using simple, direct metrics (stem density), as opposed to the more abstract metric of compositional change (trajectories in ordination space).

Spatial heterogeneity of the landscape, fire, and vegetation complicate a study of fire effects; unpredictable change in weather during prescribing burning is an additional complicating factor. It is often impractical to design a completely balanced and controlled experiment. To deal with these challenges, a field experimental protocol was created with three components. The first involved sampling more than one vegetation type in the same burn unit (block); this ensured that the vegetation types would be burned on the same day under similar weather conditions, thereby minimizing sources of variation related to weather effects on fire behavior. The second was to focus on before-after comparisons. This eliminates spatial variation that would be present in simple comparisons of treatments (burned) and controls (unburned) (Hoshmand 1994). The third was to use control plots for temporal control because the current vegetation is undergoing successional change. Therefore burned and control blocks may change in different directions if fire does have effects, or maintain the same trajectory if fire does not have any effects.

STUDY AREA AND METHODS

The study area is located in the Big Thicket region of southeast Texas, an area of about 60 by 60 km between the Trinity and the Neches Rivers. The southern boundary is about 40 km inland from the Gulf of Mexico. The area is fairly flat coastal plain that gradually becomes rolling towards the north. Elevation ranges from a few meters in the south to about 150 m above sea level in the north (USGS quadrangle sheets, 7.5 minute topographical series, provisional edition, 1984). From south to north, the Beaumont, Montgomery, Bentley, and Willis Pleistocene geological formations underlie the area. Soils in uplands and sandhills are excessively drained, poor in nutrients, and sandy. Soils of lower slopes, swamps, bottomlands, and floodplains are of loamy or clayey texture.

The area is warm and humid with a long growing season. Annual rainfall is 144 cm at Port Arthur, Texas (46-year average) in the southeast and 125 cm at Livingston (56-year average) in the northwest (1993 National Climatic Data Center data). Rainfall is evenly distributed through the year. Annual average temperature is 19.5°C (30-year average at Port Arthur).

The vegetation of the Big Thicket is quite similar to that of the rest of the Coastal Plain of the southeastern United States (Marks & Harcombe 1981; Christensen 1988; Harcombe et al. 1993) in terms of community types represented, composition within the major types, and stand physiognomy. In the Big Thicket, eleven vegetation types have been recognized and described based on physiography, physiognomy, and species composition (Marks & Harcombe 1981). Of the eleven types, seven were considered to be potentially affected by fire and therefore were sampled in this study. Roughly in the order in which they appear on a topographic-moisture gradient from dry to wet, they are as follows: sandhill pine forest (SH), upland pine forest (UP), upperslope pine-oak forest (US), midslope oak-pine forest (MS), lowerslope hardwood pine forest (LS), wetland pine savanna (WS), and wetland shrub baygall thicket (BG). Dominant species in these vegetation types are listed in Table 1. Floodplain and flatland types were not

Table 1. Dominant species in the vegetation types under study.

Vegetation Type	Dominant Species*
Sandhill Pine-Oak	*Quercus incana* Bartr., *Q. stellata* Wang, *Pinus taeda* L.
Upland Pine	*P. palustris* Mill., *P. taeda, Q. incana*
Upperslope Pine-Oak	*P. echinata* Mill., *Q. falcata* Michx., *P. palustris, P. taeda, Q. marilandica* Muenchh. *Ilex vomitoria* Ait.
Midslope Oak-Pine	*P. taeda, Q. falcata, P. echinata, Q. alba* L.
Lowerslope Pine-Hardwood	*Magnolia grandiflora* L., *Fagus grandifolia* Ehrh., *P. taeda, Q. alba, Q. nigra* L.
Wetland Pine Savanna	*P. palustris, P. taeda, Nyssa sylvatica* Marsh., *Liquidambar styraciflua* L., *Q. falcata, Magnolia virginana* L.
Wetland Shrub Baygall Thicket	*Q. laurifolia* Michx., *Nyssa sylvatica, M. virginiana, Acer rubrum* L., *Cyrilla racemiflora* L., *Ilex coriacea* (Pursh) Chapm.

* Nomenclature follows Correll and Johnston (1979).

included because fire does not play an important role in these types. Data for the LS and BG types were not included in this paper because attempts to burn the plots of these two types were unsuccessful.

Potential study sites were chosen in the Big Sandy Creek (BS), Lance Rosier (LR), and Turkey Creek (TC) units of the Big Thicket National Preserve (BTNP) and in the Roy E. Larsen Sandylands Sanctuary (RL) of The Nature Conservancy after a general field reconnaissance. The following criteria were used in study site selection: (1) presence of more than one vegetation type in a fire management unit; (2) absence of obvious recent logging or major natural disturbance; (3) site accessibility and the possibility of constructing fire breaks; and (4) burning schedules established by preserve managers.

Within a study site, plots were established in each vegetation type along a 150 m transect which traversed a uniform area of that type. Within that vegetation type, four to five 10 by 10 m^2 plots were set up in a burn block along one transect and a corresponding four or five plots were set up in a control block on a separate transect. Newly constructed firebreaks separated the burn and control blocks. Plots were located at random distances along each transect within a treatment (burn or control) block in each vegetation type. The following observations were made in each plot:

(1) Trees. Stems > 5 cm DBH (large trees) and were measured for DBH, identified by species, and tagged. Stems 2-5 cm DBH (small trees) were counted in three categories (2-3 cm, 3-4 cm and 4-5 cm) by species. Stems were considered alive if they had living tissues above breast height.

(2) Saplings. Large (DBH < 2 cm but taller than 1.4 m; shrub species were included in this category) and small (between 0.5 m and 1.4 m in height, tree species only) stems were counted in a 2 by 10 m strip centered on the central line in each plot parallel with the transect.

(3) Seedlings (< 50 cm in height, tree species only) were tallied in a 1 by 10 m strip within the sapling plot by species. Densities of seedlings and small saplings were combined in analysis.

(4) Shrubs. For clumps of these characteristically multi-stemmed woody species <1.4 m tall, cover was measured along an intercept line with a length of 10 m (in RL) or 20 m (in BTNP) in each plot parallel with the transect if 1.4 m tall). Larger shrub stems (height >1.4 m) were tallied with the large sapling class. When two plots were so close that the shrub cover measurement would overlap with that of another plot, the central line was extended accordingly in the opposite direction along the transect to avoid measurement overlap.

(5) Fuels: fine fuel (1-hour fuel) was collected in a 50 by 50 cm quadrat at one of the four corners outside the plot and sorted into duff, needles, leaves, twigs, cones, barks, and live materials. Sorted samples were dried at 70°C for 72 hours and weighed. Fuel depth was measured at 1 m, 3 m, 5 m, 7 m, and 10 m along a 10-m central line.

(6) Fire temperature: fire-sensitive tablets (Tempil of Big Three Industries, Inc., New Jersey, USA) were placed in the center of each plot to obtain a fire temperature estimate. The tablets were wrapped in aluminum foil and placed 20 cm above ground. Tablets had following discrete melting points: 52°C, 101°C, 153°C, 204°C, 262°C, 305°C, 343°C, 399°C, 454°C, 500°C, and 545°C.

For statistical analysis, a nested-factorial analysis was used to compare fire effects within types by differencing (i.e., by comparing the magnitude of change in the burn plots with the magnitude of change in the controls). About two hundred plots representing 10 sites and five vegetation types were used in this comparison (Table 2). For burn plots

Table 2. Study plots selected for within-type and cross-type comparisons.

		Vegetation Type[1]										
		WS		SH		UP		US		MS		
Unit	Site	B[2]	C[2]	B	C	B	C	B	C	B	C	Total
Big Sandy	RC[3]							5	5	5	5	20
Big Sandy	06[3]					5	5	10	10			30
Big Sandy	15					5	5	5	5			20
Big Sandy	15[3]							5	5	5	5	20
Lance Rosier	53	5										5
Lance Rosier	54	10	10									20
Turkey Creek	IS[3]			10	10			5	5	5	5	40
Turkey Creek	36[3]					5	5	10	10			30
Roy Larsen	BF[3]			5	5			4	4			18
Roy Larsen	HL	5	4	5	5							19
Total		20	14	20	20	15	15	44	44	15	15	222

[1] Vegetation type: WS—wetland pine savanna; SH—sandhill; UP—upland pine; US—upperslope; MS—midslope

[2] Treatment: B—Burn; C—Control

[3] Sites used for cross-type comparison

at two sites, there was a delay of >2 yr between measurement and burning, and so preburn values were adjusted to account for the successional change that would have taken place (based on measured changes in control plots). Changes in the control plots were generally small for large saplings and trees, but there were large fluctuations in small individuals (seedlings and saplings) and in fuel components from year to year. Because differencing increases variances of adjusted changes the small individuals were not as useful in addressing fire effects.

The before-after fire comparisons within types involved more than one site for each type; 4-5 plots were nested within each study site. In the statistical model, site and plot were treated as factors. Because there was no replication across sites within burn blocks, the error term was not retrievable. The following model was used:

$$Y_i = \text{mean} + \text{site} + \text{plot (site)} + \text{time} + \text{plot (site)} \times \text{time}$$

Where Y_i — response variable (dependent);

mean — overall mean response;

site — site effect;

time — before vs. after;

plot (site) — plot effect nested within site;

plot (site) x time — interaction between time and site;

Here the main focus is the time effect, i.e. is there a significant difference between post-fire and pre-fire measurements? Because plots were chosen randomly, effects of plot(site) and plot(site) x·time were treated as random. Because of the unbalanced experimental design (there are sets of four plots instead of five plots at some sites), a nested-factorial analysis was preferred to a repeated measurement analysis (SAS Institute; 1992a; 1992b). The two analyses produce identical results.

To test whether fire had different effects on different vegetation types, the sites that had more than one vegetation type and were burned on a single day were chosen. Six sites and four types were appropriate for such an analysis (Table 2). The four vegetation types that could be compared were sandhill, upland pine, upperslope, and midslope. Successional change unrelated to fire was adjusted for using changes in control plots as described above for the within-types comparison. However, pre-fire differences still existed for the burn plots of different vegetation types after the adjustment, and so these differences were adjusted for, as well. The reasoning was that post-fire change measured in absolute terms might not reflect the fire effects but a combination of pre-fire difference and fire effect. For instance, a reduction of 50 out of 100 small trees in an upland pine type by fire is not the same as a loss of 50 of 500 small trees in a midslope type at the same site. The former would have a 50% reduction compared to only 10% in the latter. To overcome this problem, percentage change was calculated with respect to pre-fire measurement for each site. Thus, the differences in magnitude of change between types reflected differential effects of fire on the types. The GLM procedure (SAS Institute 1992a; 1992b) was used with vegetation type as the only independent variable. Basal area, shrub cover, density of large saplings, and density of seedling and small saplings departed somewhat from a normal distribution so a logarithmic transformation to the base *e* was applied after adding one to every measurement. All transformed data appeared approximately normally distributed.

Because the response variables were from the same plots and were possibly correlated, testing the hypotheses for each variable involves multiple comparisons. Therefore, the error rates (type I error) were adjusted according to the Dunn-Sidak method (Day & Quinn 1989). Significant levels were determined by the adjusted error rate according to Dunn-Sidak method (k=8). $P<=0.0064$ (overall error rate of 0.05) was considered highly significant (**); $P<=0.0131$ (overall error rate of 0.10) was considered significant (*); $P>0.0131$ (overall error rate more than 0.10) was not significant (ns) (Figure 1).

RESULTS

Fire reduced fine fuel load in three of the five types, but not in midslope or savanna (Figure 1). Absence of significant effects in the midslope type was probably a result of cool and patchy fires (see below). In the savanna, grasses and forbs recovered quickly after fire and replaced much of the fuel consumed by fire. Fire reduced fuel depth (fine fuel only) significantly in all types, though the magnitude of reduction appeared greater in sandhill and upland pine (Figure 1). Because heavy needle drop was quite common after hot fires when the canopy was scorched, fuel consumption in the sandhill and upland types was probably greater than the data indicated.

Shrub cover was reduced significantly by fire only in the savanna; other types showed no significant differences between pre- and post-fire measurements. The rate of post-fire recovery of shrubs by resprouting was sufficient to return shrub cover to values near pre-fire values, except in the savanna type, which typically has a sparse understory. The seedling-small sapling class also showed no significant differences between pre-fire and post-fire densities, probably because of rapid resprouting.

Large saplings decreased significantly in density in all types except midslope after fire. The magnitude of the response was highest in upland pine and lowest in sandhill. The large saplings consisted mostly of post-fire survivors; few hardwood species can resprout rapidly and grow to large sapling sizes (0-1 cm DBH) in one or two years.

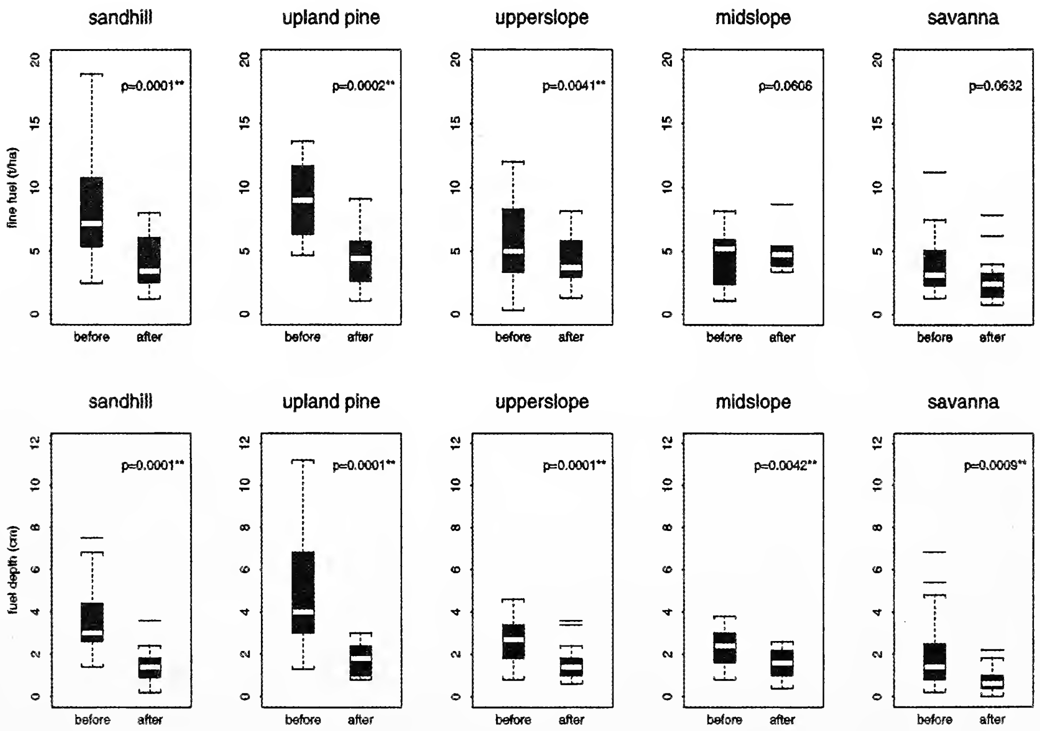

Figure 1. Boxplots of fine fuel load (upper panels) and fine fuel depth (lower panels) before and after fire for each vegetation type in within-type comparison. Vegetation types are arranged in order from dry (sandhill, upland pine) to mesic (upperslope, midslope) to seasonally wet (savanna). The box in each boxplot contains the middle half of the data; the line in the middle of a box indicates the median; the whiskers extending from the box reach to the most extreme non-outlier (brackets); outlying points are the lines above or below the bracket and plotted individually. *P*-values indicated on the panels are based on tests of nested factorial models for within vegetation type comparison.

Small tree density was significantly reduced in all types except savanna (Figure 2). Since it takes several years for saplings or seedlings to grow to small tree size, the change can be attributed exclusively to the direct impact of fire. Large tree density declined significantly in the sandhill and upland types (Figure 2). Although tree density declined, the largest trees had high survival, so tree basal area was not significantly affected by the prescription fires.

To compare changes among the types within burn, six blocks were selected (Table 2) because each of these blocks was burned on a single day, so the vegetation types being compared were burned under the same conditions. Since the post-fire values for fuel load, seedling, and saplings were a combination of fire-related death and recovery after fire rather than direct fire impact (as described above), the small tree and large tree strata were emphasized in this cross-type or between-type comparison. One block (BS10--MS and LS types) was excluded because the attempt to burn this unit failed.

For four of the six blocks, percentage changes in small tree densities due to fire differed significantly between the types ($P < 0.005$; Figure 3); two of the four also showed significant differences for percent change in large tree density, as well. The significant differences all involved comparisons between sandhill or upland pine and other types. The two blocks (BS15 and BSRC) which showed no significant differences in any of the test variables involved comparison between upperslope and midslope. The results for all six blocks suggest that fire affected two dry types (sandhill and upland pine) more strongly than it did other types.

The greater impact of fire on sandhill and upland pine corresponded to higher fire intensity. For example, the temperature readings from upland plots at BS06 were all 152°C to 399°C., whereas fire tablets melted only in two of the ten upperslope plots (152°C and 204°C). The differences in fire intensity among types in other sites were similar to BS06.

In the upperslope - midslope comparisons (BS15 and BSRC), the lack of significant differences in fire response could be a consequence of cool fires in both. At BSRC, temperatures ranged from < 52°C to 253°C; At BS15, the fire only partially burned the upperslope plots, and missed three of the five midslope plots completely.

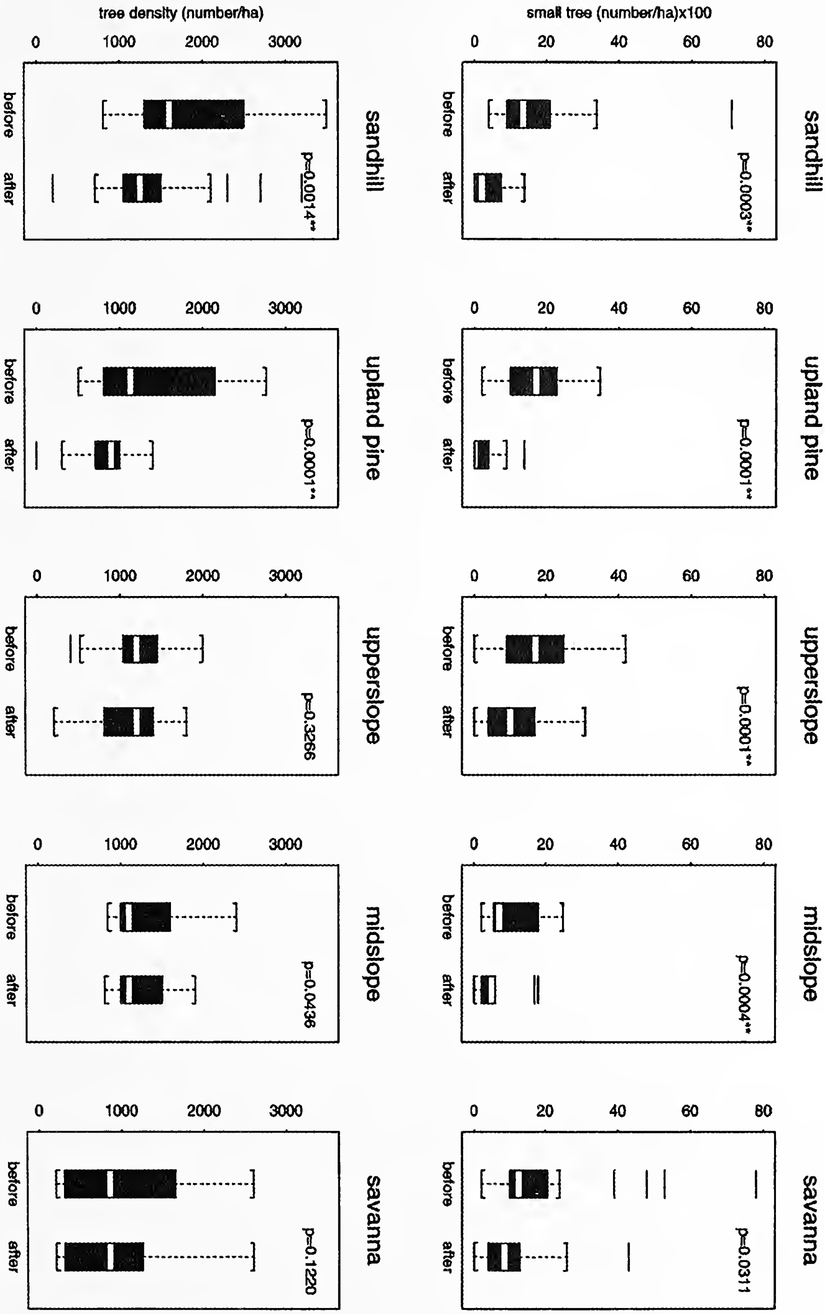

Figure 2. Boxplots of densities of small trees (upper panels) and trees (lower panels) before and after fire for each vegetation type in within-type comparison. See Figure 1 for an explanation of boxplots and significant levels and order of vegetation types.

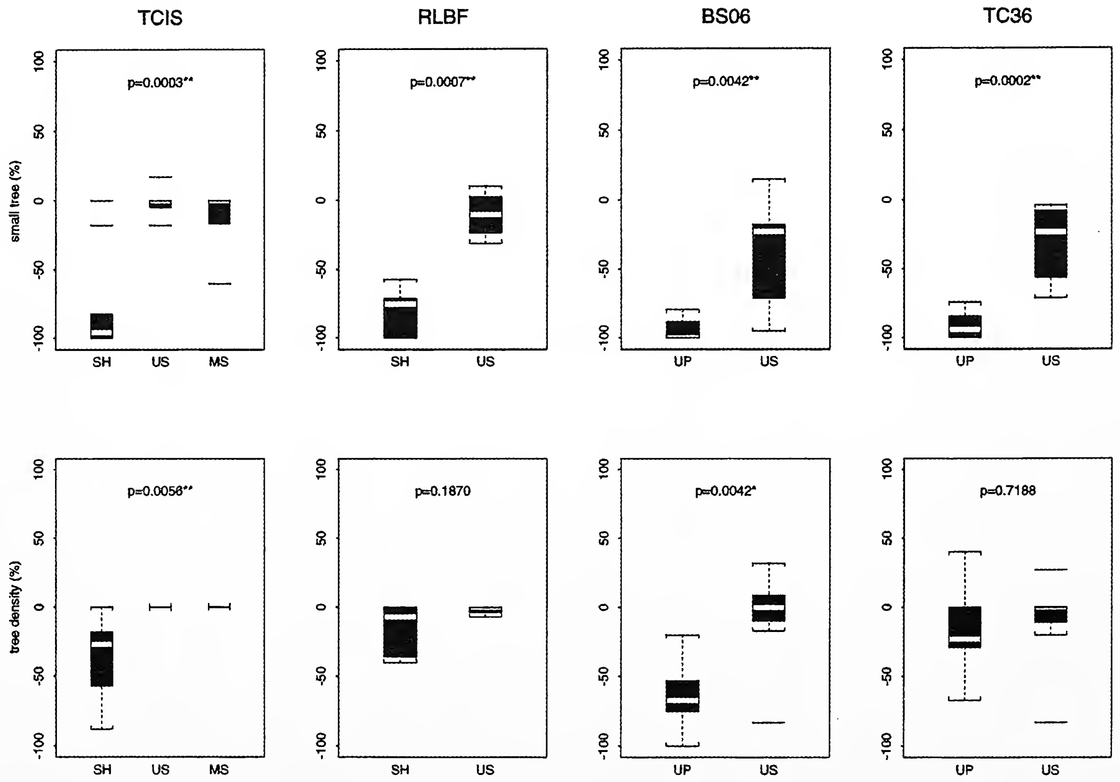

Figure 3. Boxplots of percentage change in small tree density (upper panels) and tree density (lower panels) before and after fire in cross-type comparison for each study site. Vegetation types are: SH--sandhill; UP--upland pine; US--upperslope; MS--midslope. The drier type is always on the left in each panel, and the progression of panels from left to right is from dry to mesic. See Figure 1 for an explanation of boxplots and significant levels.

DISCUSSION

The effects described here on structural characteristics of stands (reduced fuel load, reduced sapling and small-tree density, low mortality of large trees) are consistent with previous finding based on species composition change (Liu et al. 1997) that the vegetation types in Big Thicket studied were only moderately sensitive to the prescription fires. Field observations suggested that an important contributor to this modest sensitivity was rapid response of small hardwoods by regenerating and sprouting, a finding corroborated by many other studies (e.g., Abrahamson 1984a; 1984b; Westman & O'leary 1986; Malanson & Trabaud 1987; Waldrop et al. 1992).

This study focused on short-term effects of prescribed fire. How this might translate into long-term impact will depend on how the species respond to repeated fires, whether repeated fire causes a shift in species composition, and how long the short-term impacts last relative to the frequency of prescribed burning. In the slope types, fire effects may disappear in a few years because few large stems are killed by fire. In the upland types, changes will persist for many years because many small trees or even large trees were killed by fire. Whether these types will undergo conversion to longleaf pine forest with continued burning depends on changes in species composition in newly recruited seedlings and saplings, particularly the successful establishment of longleaf pine seedlings. In the current landscape, wherever the longleaf pine is still dominant, it is not difficult to change the structure and appearance of that particular vegetation type. However, at sites where the longleaf pine once was present but is now rare, such as some sandhills and upper slopes, conversion to longleaf pine forest by means of prescribed burning will be more difficult. For the midslope and lowerslope types, the intact canopy and low flammability may portend little change in the understory and future regeneration; the lack of response to fire is consistent with the idea that mixed pine-hardwood occurred on such sites in the presettlement landscape (Marks & Harcombe 1981; Harcombe et al. 1993).

In this study, modification of vegetation by fire was limited to the dry end of the topographic-moisture gradient, and so the hypothesis of differential fire effects is supported. The effect of fire on current vegetation is conditioned by that vegetation, which is influenced by site characteristics. This is consistent with a growing body of literature (e.g., Platt et al. 1989; Gibson et al. 1990; Glitzenstein et al. 1995; 2003; Breininger et al. 2002; Drewa et al. 2002). The results are also consistent with evidence that present patterns and trends in natural vegetation in the Big Thicket area are strongly influenced by soil factors, site history, and fire (Marks & Harcombe 1981; Streng & Harcombe 1982; Liu 1992; Harcombe et al. 1993; Lin et al. 2004). This work supports an approach to prescribed fire that recognizes natural patterns and natural variation in fire intensity, and thereby promotes the natural diversity of communities and the complexity of the vegetation for which the region is famous.

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TEXAS J. SCI. 56(4):335-346 NOVEMBER, 2004

GROWTH OF CHINESE TALLOW TREE (*SAPIUM SEBIFERUM*) AND FOUR NATIVE TREES UNDER VARYING WATER REGIMES

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Abstract.—Abiotic stress tolerance may play a role in the invasion and spread of Chinese tallow tree (*Sapium sebiferum*). A greenhouse experiment was conducted to determine the effects of water stress on the growth of *Sapium* and four tree species native to the southeastern United States. Species identity, water treatment, and their interaction significantly influenced growth rate and mass of seedlings. No native species had as high an average growth rate as *Sapium*. Indeed, *Sapium* had a higher growth rate than every native species in every water treatment with the exception of a single native species (*Liquidambar styraciflua* L.) in the drier treatments (pulse drought, well watered). *Sapium* exhibits the potential to thrive at any point along the water gradient present in southeastern floodplain forests.

Plant species distributions often reflect abiotic conditions. Species composition may shift along a resource gradient based on efficiency of resource use at different concentrations (Tilman 1982; 1985; Huston & Smith 1987). Species distributions in some landscapes are based primarily on one resource, and in such cases analysis of the performance of species along a gradient of that resource can be useful in predicting community composition (Tilman 1987). Similarly, comparisons of the performance of an invasive species and native species along a gradient of the most limiting abiotic factor in an ecosystem may be a good predictor of the conditions in which the invasive will displace natives (Alpert et al. 2000; Sakai et al. 2001; Daehler 2003).

Invasive species often have very different ecological attributes from species in their introduced range (Bruce et al. 1997; Busch & Smith 1995). Comparisons between native and exotic congeners (Schierenbeck et al. 1994; Mack 1996; Gerlach & Rice 2003) and between ecologically similar native and exotic species (Nijjer et al. 2002; Rogers & Siemann 2002; Daehler 2003; Siemann & Rogers 2003a) have produced informative results. Studies analyzing plant growth along a resource gradient can be useful for identifying traits that may lead to the competitive dominance of invasive species, as well as for predicting potential range expansions.

In southeastern floodplain forests, water is a major determinant of the distribution of tree species (e.g. Hall & Harcombe 1998; Wall & Darwin 1999; Denslow & Battaglia 2002; Ernst & Brooks 2003). The elevational heterogeneity of these systems positions different plant communities within close proximity to each other (Christensen 2000), which likely results in distribution of propagules into a wide range of moisture conditions, making seedling establishment and growth important aspects of population dynamics. Sloughs and depressions are often flooded year round, while other areas of bottomland forests experience seasonal flooding. Upland areas may never flood, and often experience seasonal droughts (Christensen 2000).

Tree species in these forests can be expected to follow different growth strategies depending on their distribution along a water gradient. Stress tolerance is important at extreme elevations where abiotic factors limit seedling growth and survival, while competitive ability is more important in less stressful environments. Stress tolerant species are expected to have relatively restricted phenotypic responses to external stimuli since survival depends on highly conservative growth strategies (Grime 1974; 1977; Campbell & Grime 1992). This is often reflected in slow growth rates and negligible increases in mass and growth rate in less stressful conditions (Grime 1974; 1977; Pigliucci 2001). Tree species adapted to more favorable conditions can be expected to maximize resource assimilation and grow rapidly, since biotic competition is often more important than in stressful environments (Grime et al. 1986).

A greenhouse experiment was conducted to determine the growth and performance of *Sapium sebiferum* (L.) Roxb. (Chinese tallow tree) and four native tree species under a range of water conditions representative of natural conditions. *Sapium* has invaded a variety of ecosystems in the southeastern United States. Even though it thrives in early successional conditions and has extremely high growth rates (Siemann & Rogers 2003a), seedlings are also shade tolerant (Jones & McLeod 1989; Rogers & Siemann 2002; 2003; but see Lin et al. 2004) and flood tolerant (Jones & Sharitz 1990; Conner et al. 1997, 2001).

It was predicted that the range of soil moisture conditions in which native tree species sustain high growth rates and mass production would be restricted. Adaptations to particular habitats were expected to cause tradeoffs between stress tolerance and other traits such that native species with the greatest growth rates in optimal conditions should be more sensitive to extreme conditions. Because of its widespread distribution in floodplain forests and invasive nature, *Sapium* was expected to have a higher growth rate and produce more mass than all native species under all water conditions.

METHODS

The experiment was conducted in a climate controlled greenhouse in Houston, Texas between March and August 2003. The roof and walls of the greenhouse were clear glass, and humidity was approximately 100%. *Pinus taeda* L. (loblolly pine), *Liquidambar styraciflua* L. (sweetgum), *Nyssa aquatica* L. (water tupelo), and *N. sylvatica* Marsh. var. *sylvatica* (blackgum) seeds were acquired commercially (Louisiana Forest Seed Co. Lecompte, LA). *Sapium sebiferum* seeds were collected in Texas and Georgia. In Texas, seeds were collected from many different trees at the Armand Bayou Nature Center, approximately 35 km southeast of Houston. In Georgia, seeds were collected from numerous trees on Sapelo Island, a barrier island approximately 55 km south of Savannah. Seeds of all species were germinated in topsoil in early March and transplanted into individual 11 liter plastic pots in April. Potted seedlings of each native species plus one of Texas and Georgia *Sapium* were assigned to a random position in each of twenty-four 160 liter plastic tubs (a split-plot design). Seedlings were watered daily for two weeks before initiation of the treatments.

Each tub was randomly assigned one of four watering treatments, with 6 tubs per water treatment. The treatments were: (1) Control - Pots were watered daily until water flowed out of the bottom of the pot; (2) Flooded - Pots were permanently submerged in water (1-3 cm above soil surface) for the duration of the 16-week experiment. Evaporative losses were replaced with de-ionized water to avoid salt accumulations; (3) Pulsed flood - Pots received the control water treatment for two weeks followed by flood treatment for the following two weeks. This four-week cycle was completed four times during the course of the experiment; (4) Pulsed drought - Pots received the control water treatment for the first two weeks of each four-week cycle, but received no water for the latter two weeks.

Initial stem heights, basal diameters, and leaf counts were recorded for each plant on 9 April. Stem height and number of leaves per seedling were measured weekly during the experiment. After 16 weeks, all of the plants were harvested. Roots, stems, and leaves were separated and dried at 60°C for 96 hours before dry mass was measured.

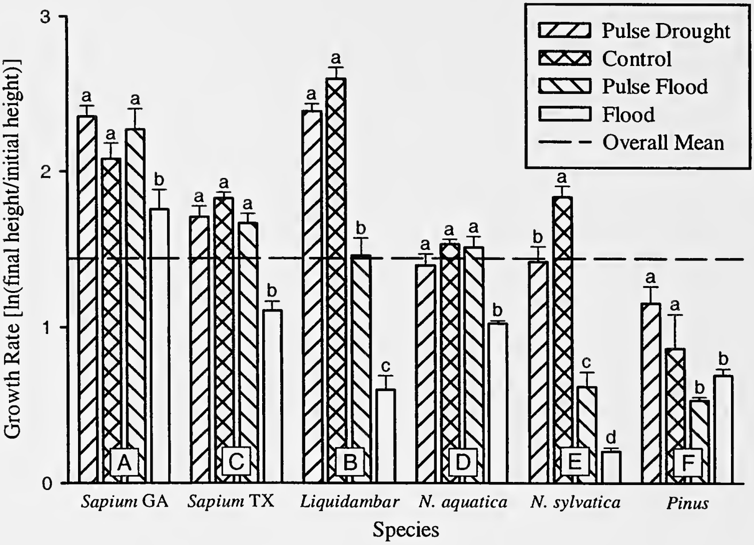

Figure 1. Dependence of the growth rate of each tree species on water treatment (mean + 1 SE). Letters indicate significantly different means ($P < 0.05$) within (lowercase) and among (uppercase) species. The mean growth rate across all species and treatments is provided as a reference.

All statistical analyses were conducted in SAS Version 8 (SAS Institute 1999). *ANOVAs* were performed using PROC MIXED to analyze the effects of species identity (split-plot factor), water treatment (whole-plot factor) and their interaction (split-plot factor) on growth rate, total biomass, and mass allocation. Stem growth rate was measured as ln (final height/initial height). Total mass was log transformed for analyses. Proportion of total mass allocated to root, stem, and leaf tissues were measured as organ mass/total mass. Fisher's Least Significant Difference (LSD) was used for means contrasts among treatments.

RESULTS

Stem growth rate depended on species ($F_{5,100} = 124.5$; $P < 0.0001$), water treatment ($F_{3,20} = 99.1$; $P < 0.0001$), and their interaction ($F_{3,100} = 18.3$; $P < 0.0001$; Fig. 1). Georgia *Sapium* grew most rapidly, followed by *Liquidambar*, Texas *Sapium*, *N. aquatica*, *N. sylvatica*, and *Pinus* (Fig. 1). Georgia *Sapium* varied the least in growth across water treatments (1.34-fold difference between treatment in which it grew fastest and the one in which it grew slowest), followed closely by *N. aquatica* (1.49-fold) and Texas *Sapium* (1.65-fold), then *Pinus* (2.17-fold), *Liquidambar* (4.34-fold), and *N. sylvatica* (9.00-fold).

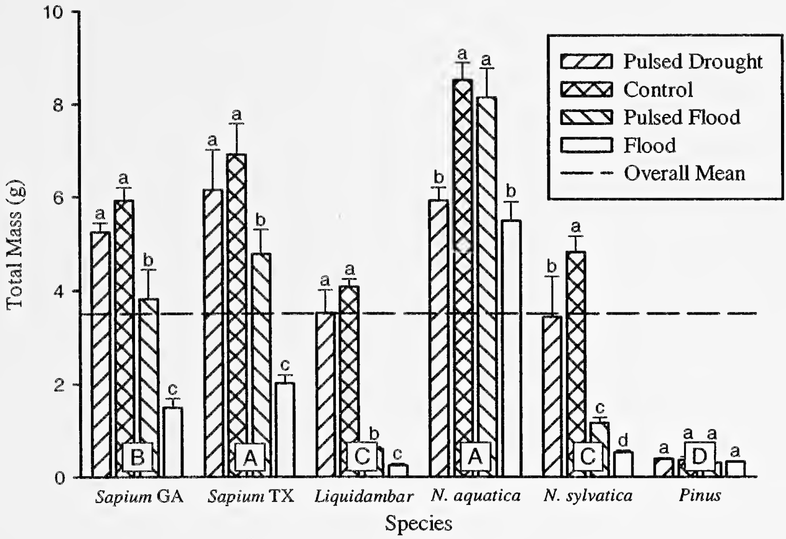

Figure 2. Dependence of total mass of each species on water treatment (mean +1 *SE*). Letters indicate significantly different means ($P < 0.05$) within (lowercase) and among (uppercase) species. The mean total mass across all species and treatments is provided as a reference.

Total mass depended on species ($F_{5,100} = 893.8$; $P<0.0001$; Fig. 2), water treatments ($F_{3,20} = 117.7$; $P<0.0001$), and their interaction ($F_{3,100} = 24.2$; $P<0.0001$; Fig. 2). *Nyssa aquatica* and Texas *Sapium* had the highest total mass (Fig. 2), but *N. aquatica* seedlings were on average between two and four times as tall as the other species at the beginning of the experiment, which likely contributed to the high final mass (Fig. 3). In a split-plot design these differences in starting sizes are difficult to account for with covariates. Texas *Sapium* had a slightly larger final mass than Georgia *Sapium*, but this can also be reconciled by initial heights (Fig. 3). *Liquidambar* and *N. sylvatica* were both significantly lower than Georgia *Sapium* but were similar with respect to each other. All species but *Pinus* exhibited significant reductions in total mass in response to permanent flooding (Fig. 2).

Proportion of total mass allocated to roots depended on species identity ($F_{5,100} = 81.4$; $P<0.0001$) but not on water treatment ($F_{3,20} = 1.2$; $P = 0.35$) or their interaction ($F_{3,100} = 1.8$; $P = 0.10$). Proportional leaf mass depended significantly on both species identity ($F_{5,100} = 198.6$; $P<0.0001$) and water treatment ($F_{3,20} = 5.54$; $P<0.01$) but not on their interaction ($F_{3,100} = 0.46$; $P = 0.94$). Stem mass proportion

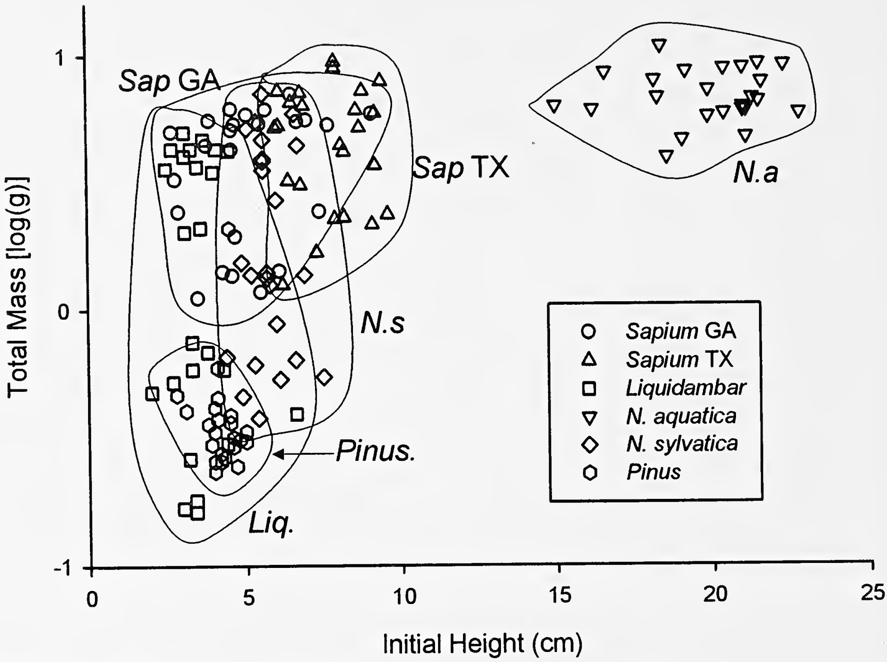

Figure 3. Initial height at planting versus log (total mass) for each species.

was significantly affected by species identity ($F_{5,100} = 349.2$; $P<0.0001$) and the interaction between species identity and water treatment ($F_{3,100} = 15.1$; $P<0.0001$), but not water treatment alone ($F_{3,20} = 0.7$; $P = 0.54$). *Sapium* seedlings allocated approximately 30% of mass to leaves, 30% to stems and about 40% to roots. *Nyssa aquatica* had a root to shoot ratio similar to *Sapium*, but allocated markedly less mass to leaves. *Liquidambar* and *N. sylvatica* were similar to each other in their stem versus leaf allocation ratios, but *N. sylvatica* had the highest root to shoot ratio of any species, while *Liquidambar* allocated a relatively low amount of mass belowground. *Pinus* had the lowest root to shoot and stem to leaf ratios (Table 1).

DISCUSSION

The results of this experiment suggest that *Sapium* has characteristics of both stress tolerant and rapidly growing species without experiencing the same magnitudes of tradeoffs between these characteristics as are evident for the native tree species in this study. *Sapium* had high growth rates across all water treatments and experienced only modest

Table 1. Proportion of total mass allocated to root, stem, and leaf parts by species.

	% Total Mass		
Species	Root	Stem	Leaf
Sapium GA	39	31	30
Sapium TX	42	28	30
Liquidambar	31	27	42
Nyssa aquatica	37	45	18
Nyssa sylvatica	44	21	35
Pinus	26	16	58

reductions in growth in response to water stress (Figs. 1, 2). *Sapium*'s stress tolerance appears to extend across the entire experimental water gradient. Within this range of tolerance, *Sapium*'s growth rate was always high relative to most native species. The only species that grew faster than *Sapium* was *Liquidambar* in drier treatments, and it was a very poor performer in the flood treatment (Fig. 1).

While *Sapium* may not be able to out perform *N. aquatica* in permanently flooded conditions if differences in initial seedling sizes observed here are typical of field conditions (Fig. 2), *Sapium* seedlings may still survive to reproductive maturity due to relatively low competition in such stressful environments (Ernst & Brooks 2002). The high leaf-to-stem mass ratio of *Sapium* relative to *N. aquatica* also indicates that *Sapium* may be able to survive in very wet areas with dense canopies in which *N. aquatica* may not be able to capture enough light to grow well (Jones & Sharitz 1990). *Sapium* should also be able to exist in the middle-to-high moisture range of *Liquidambar* and *N. sylvatica*. In areas that are highly favorable for either of the natives, *Sapium*'s shade tolerance (Rogers & Siemann 2002; 2003) and ability to reproduce as a sub-canopy species may favor its presence. The performance of *Sapium* in areas with drier moisture regimes was not tested in this study, but it has been shown to be much less successful in dry uplands that support *Liquidambar* and *N. sylvatica* (Hall & Harcombe 1998; Harcombe et al. 2002; Lin et al. 2004).

Sapium also exhibited positive traits similar to *Liquidambar* and *N. sylvatica*. High growth rates in non-flood treatments (Fig. 1) and high leaf-to-stem ratios (Table 1) of these two natives are indicative of seedlings adapted to relatively nutrient-rich, disturbed areas (Grime 1974; 1977). *Nyssa sylvatica* had high root : shoot ratios (Table 1) and relatively greater mass production in flood treatments (Fig. 2) indicating that seedlings of this species may survive periods of flooding and grow rapidly when floodwaters subside (Grime et al. 1986). *Liquidambar* performed as a more typical gap species, allocating more resources to stem growth rate in a relatively narrow range of dry to moist soils (Fig. 1, Table 1). *Sapium* exhibited growth traits that were characteristic of these two native species including high root to shoot ratios, intermediate leaf to stem ratios, and high growth rates (Table 1).

The potential gradient distributions of native seedlings in this experiment corresponded relatively well with observed distributions of mature trees. *Nyssa aquatica* was clearly the most tolerant of both flood treatments. Mature *N. aquatica* trees often coexist with *Taxodium distichum* (L.) Rich. as the dominant species in anoxic bottomlands (Marks & Harcombe 1981; Visser & Sasser 1995). *Nyssa sylvatica* seedlings can likely survive periodic flooding while taking advantage of intermittent dry periods, as well as thrive in moist areas. Distribution of mature individuals of this species also covers a wide range of moisture conditions, including areas with seasonal flooding and drought (Keeland et al. 1997). *Liquidambar* performed best in moist to dry conditions, which does appear to deviate slightly from the observed distribution of mature trees. *Liquidambar* is primarily a floodplain species (Marks & Harcombe 1981; Denslow & Battaglia 2002; Ernst & Brooks 2003), but the drought treatment in this experiment was not severe enough to simulate upland conditions. Therefore, dry conditions in this experiment are similar to more elevated areas within a floodplain. Light may also play an important role in the distributions of *Liquidambar* and *N. sylvatica*. Their strategy of maximizing shoot growth in this study is an adaptation consistent with these species being shade intolerant (Hall & Harcombe 1998; Lin et al. 2004). The high variability of total mass and mass allocation under varying water regimes also indicates that these species maximize growth under relatively specific, favorable conditions. *Pinus* was more flood tolerant in this study than was expected (Kozlowski 1997) and was relatively incongruous with respect to distribution of mature trees. Light availability is another important predictor of *Pinus* distribution in nature, which may explain this discrepancy (Harcombe et al. 2002). The apparent flood tolerance may also be a reflection of the fine-grained soils used in this study, which may have stunted the growth of seedlings in all water treatments.

It is not clear what mechanism would contribute to the superior performance of the invasive species observed in this study. One possibility is that *Sapium* possesses novel physiological or biochemical traits as a result of taxonomic novelty or an evolutionary history in a different biotic province or under different selection pressures (Tilman 1999). This possibility cannot be discounted. *Sapium* is unusual in that it is the only tree in the southeastern U.S. that is a member of the Euphorbiaceae. In addition, *Sapium* is the only plant from Asia in this study, and it is possible that in general Asian trees would outperform North American trees in this type of experiment. Finally, *Sapium* has a long history of being cultivated in Asia for its oil rich seeds, and was originally introduced to the U.S. as an agricultural crop (Bruce et al. 1997). The traits observed here could be the result of artificial selection prior to introduction to North America. There are, however, proximate ecological factors that contribute to the success of invasive plants that may have relevance to the results of this experiment.

Low herbivore loads in the introduced range is one of the factors that is widely believed to contribute to the greater vigor of exotic plants (Keane & Crawley 2002), and has been shown to contribute to *Sapium*'s success (Rogers & Siemann 2002; Siemann & Rogers 2003a). One way in which plants may benefit from low herbivore loads is by a plastic phenotypic response to low losses to herbivores in which additional resources are used for growth (Elton 1958). In this greenhouse study, however, there was negligible damage to any plants, either natives or *Sapium*, so this is unlikely to be the cause of *Sapium*'s unusual combination of high growth rates and high flood tolerance observed here. In fact, *Liquidambar*, the only species that was able to outperform *Sapium* in this study, sometimes suffers extremely high herbivore damage in natural settings (Siemann & Rogers 2003a) which would only strengthen the conclusion that *Sapium* has an unusual combination of growth and tolerance to stress.

Release from herbivory may also affect plant performance by directional selection on plant defense and growth (Blossey & Nötzold 1995). *Sapium*'s high level of vigor in a wide range of conditions may be due to genetic responses to low herbivory resulting in reallocation of resources from defense to faster growth (Siemann & Rogers 2001, 2003b) and perhaps also to phenotypic plasticity (Bazzaz et al. 1987, Alpert et al. 2000). If this is true, the tradeoff between growth rates and stress tolerance examined in this study may be applicable to plant responses under varying conditions of other resources and other forms of stress. Comparisons of the results of a greenhouse study such as this and natural distributions may give insights into the role of other factors, such as herbivory, in determining plant distributions.

This study adds further support to the importance of stress tolerance in the invasion of southeastern floodplain forests by *Sapium*. The two primary determinants of species distribution in these forests are light and water (Hall & Harcombe 1998). Other studies have demonstrated *Sapium*'s ability to grow in a variety of light levels (Jones & McLeod 1989; Rogers & Siemann 2002; 2003; Siemann & Rogers 2003c). In accordance with other studies on soil moisture regimes (Jones & Sharitz 1990; Barrilleaux & Grace 2000; Conner et al. 2001), this experiment confirms that *Sapium* can perform well under a wide range of water conditions. Regardless of the mechanism, *Sapium* is able to exhibit traits of both rapidly growing and stress tolerant species, which may allow it to spread into bottomlands with anoxic soils as well as into seasonally dry areas of floodplain forests. Perhaps more importantly, this study demonstrates the ability of an introduced species to minimize tradeoffs that substantially affect the performance and growth strategies of native species.

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TEXAS J. SCI. 56(4):347-356 NOVEMBER, 2004

EFFECTS OF TEMPERATURE AND MULCH DEPTH ON CHINESE TALLOW TREE (*SAPIUM SEBIFERUM*) SEED GERMINATION

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Abstract.—Shredding mowers can be used in prairie and savannah restoration to quickly eliminate trees, such as the invasive Chinese tallow tree (*Sapium sebiferum*), and leave a layer of mulch on the ground. *Sapium* has shown highest germination rates in fluctuating daily temperatures, and mulch has been shown to damp those fluctuations in the field. A lab study was conducted to separate direct effects of mulch depth and indirect effects from changes in soil temperatures on *Sapium* seed germination. *Sapium* seeds were exposed to different combinations of mulch depth and temperature oscillations. *Sapium* seeds showed highest germination in large temperature oscillation treatments regardless of the depth of the mulch. Seedlings were able to emerge through mulch up to 10 cm deep, the maximum used in this study. While herbicide use appears to be necessary because of resprouting from stumps, this study indicates that mulching *Sapium* trees shows promise as a restoration tool by removing existing trees as well as by reducing *Sapium* regeneration from seed through the indirect effects of mulch on seed germination. The lower subsequent seedling numbers might reduce the frequency and intensity of future herbicide treatments.

The invasive Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.), Euphorbiaceae, was introduced to the United States from Asia in 1772 and has spread across the southeastern states (Barrilleaux & Grace 2000; Bruce et al. 1997). Grasslands have always been subject to woody encroachment, but the great seed output, bird dispersal, rapid growth, and adaptation to wide environmental conditions of *Sapium* (Renne & Gauthreaux 2000; Rogers et al. 2000; Siemann & Rogers 2003a) have allowed it to become the most serious threat to endangered prairies along the upper coast of the Gulf of Mexico (Grace 1998). Once *Sapium* becomes established, it shades out the native herbaceous vegetation and forms a monospecific forest (Bruce et al. 1997; Siemann & Rogers 2003b). This also displaces native animal species, such as several federally endangered grassland birds (Herkert et al. 2003; Perkins et al. 2003). The loss of prairie bunchgrasses and rapid decomposition of *Sapium* litter (Cameron & Spencer 1989) leave the soil bare beneath the trees; such a condition may reduce bioremediation of anthropogenic pollutants and speed the flow of water and sediments to rivers (Fajardo et al. 2001; Harbor et al. 1995; Liaghat & Prasher 1996).

Sapium invasion is not limited to prairies. A 20-yr forest dynamic study (Harcombe et al. 1999) revealed that *Sapium* had increased dramatically in the Neches Bottom Unit of the Big Thicket National Preserve between 1981 and 1995. Among small saplings, *Sapium* growth was three times the median of all species studied during that period, and among large saplings, *Sapium* growth significantly exceeded that of all other species. In another study of the area, Hall & Harcombe (1998) documented an interaction of shade tolerance and flood tolerance among the species present. For example, species often were found in higher light conditions than would be expected from their known tolerance for shade, apparently having to make environmental trade-offs to survive both stresses of shade and flooding. Since *Sapium* is known to perform well in shade (Jones & McLeod 1989; Rogers 2002) and withstand flooding (Conner 1994; Grace 1998), it may become a serious threat to native tree species in the Big Thicket.

Effective control for *Sapium* has been elusive, and a great percentage of coastal prairie has been displaced by this exotic species. A promising new technique for prairie restoration uses shredding mowers to mulch stands of *Sapium*. This method employs a large shredding mower to chip entire trees at ground level. Herbicide is manually applied to the cut surface of the stumps to reduce resprouting. For restoration to be successful, *Sapium* regeneration needs to be controlled while simultaneously promoting native prairie plant regeneration. Mulch from *Sapium* trees may contribute to successful prairie restoration by limiting *Sapium* regeneration from seed. However, mulch depths necessary for suppression of *Sapium* seed germination and the mechanisms that contribute to suppression are not known.

Armand Bayou Nature Center, located 44 km southeast of Houston, Texas, has twice mulched *Sapium* trees on invaded prairie with a shredding mower, once in summer of 2000 and again in fall 2002/spring 2003. In the 2000 restoration, the stand was more mature and resulting mulch depths ranged up to 15 cm. In the younger stand mulched in 2002/2003, average mulch depths were approximately 5 cm. The subsequent emergence of *Sapium* seedlings in the area mulched in 2000 appeared lower than in the area where *Sapium* trees were killed with herbicide and left standing.

The mulch layer might have reduced germination by limiting day/night variation in surface soil temperatures. Experimental studies have shown highly variable germination rates for *Sapium*, depending on the geographic source of the seeds (Cameron et al. 2000) and the germination protocols. Conway et al. (2000) only achieved 0-10% gemination on filter paper in petri dishes under an oscillating light and temperature regime, but Cameron et al. (2000) and Renne et al. (2001) achieved 26% and 22.5% gemination rates, respectively, for seeds planted in soil in greenhouses under natural temperatures and light. Seeds under these conditions would be expected to experience natural daily fluctuations in soil temperatures. In another study, highest germination rates were obtained for seeds planted in soil under experimentally controlled fluctuating daily temperatures (Nijjer et al. 2002).

The objective of this lab study was to separate direct effects of mulch and indirect effects by changes in soil temperatures on *Sapium* seed germination by maintaining constant temperature regimes under varying mulch depths. If direct effects of mulch on seed germination are the primary cause of lower germination rates, then germination should decrease as mulch depth increases for all temperature treatments. However, if indirect effects *via* changes in soil temperatures are more important, germination should be greatest in high oscillating temperatures regardless of the mulch depth.

MATERIALS AND METHODS

Seeds of *Sapium* were collected from trees at the University of Houston Coastal Center in Galveston County, Texas, from August to September, 2002 and stored at room temperature. On 16 July 2003, 50 seeds were planted in each of 48 plastic bins (16 by 30 by 10 cm deep) on a 2.5 cm layer of commercially available topsoil and covered with another 2.5 cm layer of topsoil. Bins were randomly assigned to a temperature treatment (high oscillation, low oscillation, warm, and cool) and a mulch treatment (bare soil, 5 cm *Sapium* mulch, and 10 cm *Sapium* mulch) in a full-factorial design. Temperature treatments were chosen based on field soil temperatures measured during spring 2003 in the field that was mulched in late 2002 (Fig. 1). Bins were in a temperature controlled room (21°C) without windows or artificial light for the duration of the experiment. *Sapium* germination is independent of light conditions (Nijjer et al. 2002).

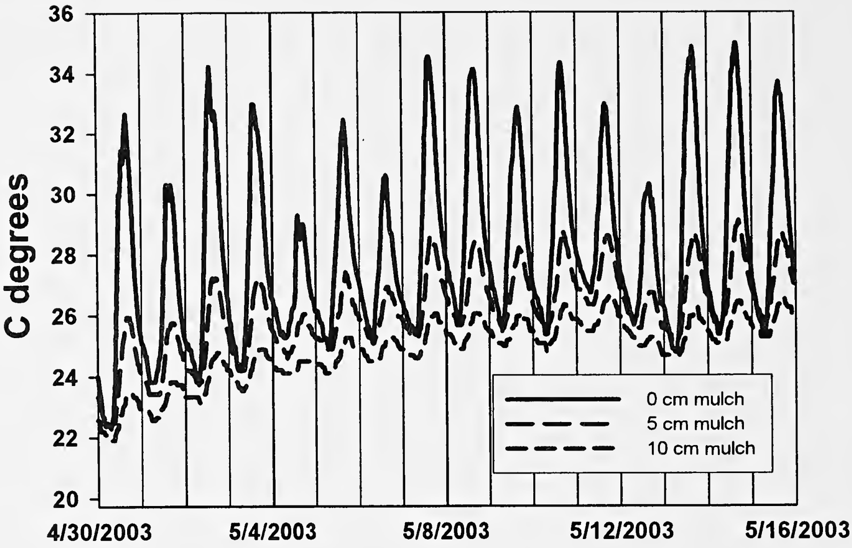

Figure 1. Sample of field soil temperatures recorded every 30 minutes, by mulch depth, in a field that had *Sapium* trees removed with a shredding mower in late 2002. Vertical bars indicate midnight on successive days.

Electric roof de-icing cables (EASYHEAT, New Carlisle, IN) laid in the bottoms of the bins raised the soil temperatures. Cables passed once through low-oscillation bins and twice through high-oscillation and warm bins. Oscillation treatments were warmed for 16 hours and allowed to return to room temperature over eight hours. The high oscillation temperature maximum was 33°C, and the low oscillation temperature maximum was 27°C. The warm treatment was a constant 33°C, and the cool treatment was constant room temperature (21°C).

Fresh *Sapium* mulch was collected from a recently mulched *Sapium* restoration area at Armand Bayou Nature Center. Mulch was spread evenly across the soil in the 5 cm and 10 cm mulch treatment bins. Plastic baffles were used to support the mulch layer at the edges of the 10 cm treatment bins. Because the 0 cm and 5 cm mulch treatments lost more heat to the air than the 10 cm mulch treatment and did not maintain the desired soil temperatures, heavy-duty plastic sheeting was cut slightly larger than each bin and laid over the tops of the bins for these two treatments. The plastic was neither sealed to the bins nor in contact with the soil or mulch layers.

Table 1. Dependence of *Sapium* germination on experimental temperature and mulch depth treatments in an *ANOVA*.

Factor	*df*	SS	*F*-value	*P*-value
Temperature	3	112.2	123.5	<0.0001
Mulch Depth	2	2.0	3.4	<0.05
Temperature*Mulch	6	3.5	1.9	0.11
Error	36	10.9		

All treatments were thoroughly watered three times each week until water drained from the bins, and newly germinated seeds were counted and removed from the bins during these periods. The experiment was conducted for 125 days, but no seeds germinated after 110 days.

ANOVA was used to compare the different experimental treatments and Fisher's LSD tests were used for post-hoc means contrasts (Statview 5.0, SAS Institute, 1998, Cary, North Carolina). Data were checked for normality and square root transformed to meet the assumptions of *ANOVA*. Data were back-transformed for presentation.

RESULTS

Temperature treatment and mulch depth treatment, but not their interaction, had significant effects on seed germination; however, temperature alone explained 87% of the variation in germination (Table 1). All pairwise comparisons among temperature treatments were significantly different (*P* ranging from <0.0001 to 0.0152) with the greatest germination in the high oscillation (217 germinants from 600 seeds total) followed by low oscillation (34 germinants), warm (18 germinants) and cool (1 germinant) treatments (Fig. 2). The only significant difference among mulch treatments was the lower germination rate under 5 cm of mulch compared to bare soil (Fig. 2).

DISCUSSION

Germination success for *Sapium* clearly depends on daily fluctuations in temperature, and the amplitude of the fluctuation is critical, as evidenced by the magnitude of the difference between germinants in the high-oscillation treatment and the low-oscillation treatment (Fig. 2). Pioneer species and wetland species commonly use diurnal temperature fluctuations as an indicator of canopy gaps (Fenner 1985; Baskin & Baskin 1989), proximity to the soil surface (Thompson & Grime 1983;

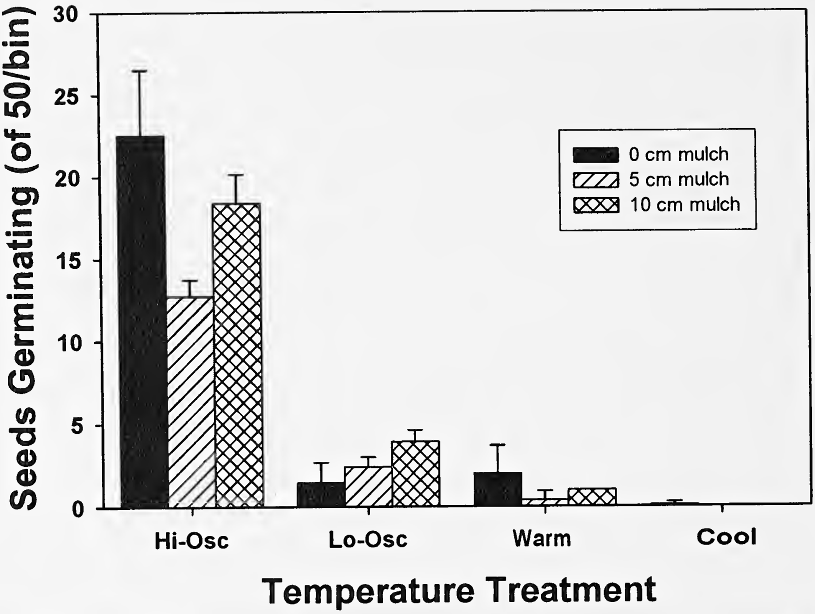

Figure 2. Number of *Sapium* seeds germinating in each bin (means + 1 *SE*) for each combination of temperature treatment (Hi-Osc = 21-33°C, Lo-Osc = 21-27°C, Warm = constant 33°C, Cool = constant ambient 21°C) and mulch depth (0 cm, 5 cm, 10 cm).

Ghersa et al. 1992), or recession of standing water (Fenner 1985). These environmental conditions are often critical to subsequent seedling success (Thompson & Grime 1983; Fenner 1985; Vleeshouwers et al. 1995).

Several studies of invasive species have shown dependence on temperature fluctuations for successful germination (Ghersa et al. 1992; Lonsdale 1993; Young & Clements 2001). Also, several threatening invasives are woody invaders of wetland areas, including *Sapium* (Davis et al. 1946; Bruce et al. 1997), *Schinus terebenthifolius* Raddi, or Brazilian peppertree (Wheeler et al. 2001; Hight et al. 2003), and *Melaleuca quinquenervia* (Cav.) Blake, or punktree (Costello et al. 2003; Johnston et al. 2003). Mulching might be an effective control method for other invasive woody species as well.

Germination and emergence from under 10 cm of mulch was not significantly different from that from bare soil ($P = 0.6575$), and there was no consistent trend in germination rates as mulch depth increased. This supports a conclusion that the indirect effect of mulch on soil temperature oscillations is more important than mulch depth alone for *Sapium* seed germination. It is encouraging for the potential success of this restoration method that only 5 cm of mulch in the field was required to damp the soil temperature oscillations sufficiently (Fig. 1) to achieve the germination suppression evidenced by the low oscillation treatment in Figure 2.

The cotyledons of the seedlings in 10 cm of mulch were on long attenuated stems. The large *Sapium* seed (0.16 g/seed, Bonner 1989) apparently provides adequate resources for the seedling to emerge through deep mulch before reaching light where it can begin to photosynthesize. Several studies in different environments have shown a positive correlation between seed mass and ability for seedlings to become established (Dzwonko & Gawronski 2002; Christie & Armesto 2003). When they modeled the emergence response of weed seeds to burial depth, Grundy et al. (2003) also found that some species had adequate reserves to emerge from a wider range of depths than might be expected in the field, as *Sapium* demonstrated in the present study. This may contribute to *Sapium*'s ability to invade and exploit many different environmental conditions.

To be useful, the mulching treatment should have minimal effects on native prairie species. Foster & Gross (1998) found that prairie forbs and the prairie grass, *Andropogon gerardi*, were able to establish a significant number of seedlings in intact plant litter, even though the densities in litter were significantly lower than where litter was removed. In multiple-site studies, Foster & Gross (1997) and Foster (1999) found that accumulated litter affected *Andropogon gerardi* seedling establishment in some sites but not in others. Also, when examining tallgrass prairie recolonization mechanisms after soil disturbance by pocket gophers, Rogers & Hartnett (2001) found that vegetative regrowth after burial under soil was the dominant recolonization mechanism. Therefore, possible mulch-induced seed germination suppression could be expected to have little impact on native vegetation. Finally, the high flotation rubber tires of the mulching equipment limit damage to the root structure of existing perennial vegetation.

Techniques for control of invasive vegetation include biological, herbicidal, mechanical, or some combination of these. While herbicide use appears to be necessary because of resprouting from stumps (Jubinsky & Anderson 1996), this study indicates that mulching live trees can be an effective initial mechanical treatment that reduces subsequent seedling numbers, and thereby reduces the frequency and intensity of herbicide treatments.

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THE EFFECT OF MYCORRHIZAL INOCULUM ON THE GROWTH OF FIVE NATIVE TREE SPECIES AND THE INVASIVE CHINESE TALLOW TREE (*SAPIUM SEBIFERUM*)

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Abstract.—Mycorrhizal fungi may play an important role in plant invasions, but few studies have tested this possibility. Chinese Tallow (*Sapium sebiferum*) is an invasive tree in the southeastern United States. An experiment was conducted to examine the effects of mycorrhizal inoculation, fungicide application, and fertilization on the growth of *Sapium* and five native tree species (*Liquidambar styraciflua*, *Nyssa sylvatica*, *Pinus taeda*, *Quercus alba*, and *Q. nigra*) that co-occur in forests in the Big Thicket National Preserve in east Texas. Seedlings were grown in a greenhouse for twenty weeks under full factorial combinations of mycorrhizal inoculum, fungicide, and fertilizer. Mycorrhizal inoculation increased *Sapium* growth but caused zero to negative growth changes of the five native species. This suggests that *Sapium* may gain unusual benefits from mycorrhizal associations. *Liquidambar styraciflua* benefitted from mycorrhizal inoculation only in fertilized conditions which indicates that the potential advantage *Sapium* might gain from mycorrhizal associations may vary with native species and soil fertility.

Mycorrhizal fungi form close associations with roots of plants in which in exchange for fixed carbon, the fungi provide essential nutrients to the plant (N, P) and may protect the plant from pathogens, support helpful bacteria, enhance soil aggregation, assist in water transport and gain, and stimulate plant growth through auxin production; these associations can vary from mutualistic to parasitic depending on soil fertility levels (Harley 1968; Allen 1991; Johnson et al. 1997; Smith & Read 1997; Van der Heijden & Sanders 2002). It is possible that mycorrhizae play a key role in temperate forest dynamics and community responses by changing the outcome of competition and by influencing plant fitness (Johnson et al. 1997; Van der Heijden & Sanders 2002). Little attention has focused on how the existing mycorrhizal network of the introduced range may facilitate the invasion of exotic plant species.

Sapium sebiferum (L.) Roxb, a native to central China, was introduced to Georgia in the late 18th century (Bruce et al. 1997). Although present in Texas in the early 1900's, *Sapium* did not become invasive until the middle of the century and has only rapidly increased abundance in the past two decades in mesic and hydric forests in the Big Thicket National Preserve (BTNP) in east Texas (Harcombe et al. 1999). Recent studies have shown that *Sapium* benefits from low herbivore loads (Siemann & Rogers 2001; 2003ab; Rogers & Siemann 2002; 2003), but *Sapium* appears to have unusually high growth rates even after accounting for differences in aboveground herbivore impacts. Although a release from belowground pathogens could explain the high growth rates of *Sapium*, unusually large benefits from mycorrhizal associations are also a factor that may contribute to *Sapium*'s invasive success.

Generalist mycorrhizae with low host specificity may be able to form associations with invasive plants (Richardson et al. 2000). This association by itself would not create unusually high benefits, and thus could not be itself responsible for invasive success, unless the invader could utilize the mycorrhizae in a novel fashion (Richardson et al. 2000). The combination of potentially novel mycorrhizal utilization and the short co-evolutionary history exotic plants have with native mycorrhizal mutualists suggests that these plants could receive unusually high benefits or extremely high costs their introduced ranges (Richardson et al. 2000). Another way that exotic invaders could obtain benefits would be to usurp native species' existing mycorrhizal network connections, or utilize neighbors' nutrient pools with their own extraradical (soil exploring) hyphae, thus parasitizing neighboring competitors through enhanced nutrient uptake (Marler et al. 1999; Zabinski et al. 2002). Only limited work to date has been done to examine how the existing mycorrhizal network of the introduced range may influence the competitive ability of exotic invaders (Bray et al. 2003). Understanding how *Sapium* utilizes mycorrhizal associations in its introduced range may help explain the mechanisms underlying its invasion in the BTNP and increase general knowledge of the role of mycorrhizae in affecting plant community dynamics.

A greenhouse experiment was conducted to test the effects of mycorrhizal inoculation, fungicide application, and fertilization on the growth of *Sapium* and five tree species native to the BTNP. If mycorrhizae contribute to *Sapium* invasion, then the performance advantage of *Sapium* compared to natives should be greater with mycorrhizal inoculation than without. To potentially decrease the performance advantage of *Sapium* if mycorrhizal inoculation facilitates invasion, Rovral fungicide was applied (Gange et al. 1990; Ganade & Brown 1997). Fertilization is predicted to highlight plant alterations in mycorrhizal dependencies and mimic potential changes in field conditions. Fertilization is predicted to decrease the effect of mycorrhizae on plant performance because carbon costs are not offset by benefits of nutrient gathering in high fertility (Menge et al. 1978; Buwalda & Goh 1981; Hetrick et al. 1988; Hetrick 1991; Johnson 1993; Peng et al. 1993) and additionally because the benefits plants receive from mycorrhizae may be less valuable in higher fertility conditions (Koide 1991; Johnson 1993; Johnson et al. 1997). In Flatland Hardwood Pine Forests of the Lance Rosier Unit in the Big Thicket, which are equivalent to Lower Slope Hardwood Forests found elsewhere, phosphorus tends to be in limited supply (Marks & Harcombe 1981; Knox et al. 1995; BTNP 2003) because of its difficulty to acquire at low levels and strong adsorption to soil particles (Nye & Tinker 1977; Read 1991). However, nitrogen deficiencies may limit growth of plants with non-mycorrhizal affiliations because they can only absorb simple forms of N (Chalot & Brun 1998). Together these predictions will begin to answer how mycorrhizae may promote or hinder *Sapium's* invasibility and ultimately alter the surrounding native community.

METHODS

Seeds of five native tree species that are common in mesic and hydric forests in the BTNP and may potentially be outcompeted by *Sapium sebiferum* (*Liquidambar styraciflua* L. [sweetgum], *Nyssa sylvatica* Marsh [blackgum], *Pinus taeda* L. [loblolly pine], *Quercus alba* L. [white oak], and *Q. nigra* L. [water oak]) were purchased (Louisiana Forest Seed Company, Lecompte, LA) to ensure that seeds were from uniformly healthy trees. *Sapium sebiferum* seeds were collected at Armand Bayou Nature Preserve (Houston, TX). Stratification took place in a 21°C cold-room in January-February 2003. Germination of non-surface sterilized seeds occurred in an unheated greenhouse on the Rice University campus during March-May 2003. Germinated seeds were planted in 66 mL Conetainers (Stuewe & Sons, Inc., Corvallis, OR) filled with potting soil.

Forty-eight similarly sized seedlings of each species were selected approximately two weeks after germination. All of the plants within each species were randomly assigned to one of eight treatments in a full-factorial experimental design with inoculation (yes or no), fungicide (yes or no) and fertilizer (yes or no) for a total of six replicates per treatment. Roots were gently brushed free of soil and the soil was retained. Roots were then dipped in either "Silva Dip" (Reforestation Technologies International, Salinas, CA) which contained a total of eight general endo- and ectomycorrhizal species (*Glomus intraradices*, *Glomus* *aggregatum*, *Glomus mossae*, *Pisolithus tinctorius*, and four species of *Rhizopogon* sp.) or distilled water. Excluding *Rhizopogon* sp., which is primarily found in the northwestern United States, at least one of the remainder of the endo- and ectomycorrhizal species listed would be encountered by the focal tree species of this study in the field (Keeley 1980; Black et al. 1981; McIntosh et al. 1985; Weber & Smith 1985; Walker & McLaughlin 1991; Metzler & Metzler 1992; Lewis & Strain 1996; Constable et al. 2001). After dipping, roots were covered with the retained soil and transplanted into 3.8 liter Treepots™ (Stuewe & Sons, Inc.) filled with a mixture of 2/3 potting soil and 1/3 perlite. Pots were placed within blocks grouped by species on plastic pallets on the greenhouse floor because of differences in germination times. Pots were watered as needed and periodically rotated within species blocks to minimize shading and location effects.

Fertilizer was applied four times in the course of the 20-week experiment in weeks 3, 7, 12, and 17. Application rates were equivalent to 4 g/m^2 each of N, P and K per application. This mimics field regulation standard rates. Nutrients were added as ammonium nitrate (N), superphosphate (P), and potash (K) dissolved in 40 mL of distilled water. Distilled water was added to non-fertilized controls.

Rovral® 4 Flowable Fungicide (Aventis CS, Bridgewater, NJ) was applied three times in the course of the 20-week experiment in weeks 4, 10, and 16. Rovral, active ingredient iprodione, has been shown to reduce mycorrhizal infection in plant roots and is a contact pesticide with no known systemic action (Gange et al. 1990; Ganade & Brown 1997). Application rates followed recommendations for controlling pathogenic root fungi (Aventis 2001).

Initial height of each seedling was measured. Initial heights were taken before seedlings were dipped into either inoculum or a distilled water control and as such did not require sterilization of equipment to pre-empt transfer of inoculum between sources. At the end of 20 weeks, roots, leaves, and stems were harvested and dried at 60°C for at least 72 hours before weighing.

An *ANCOVA* with starting height as a covariate was used to test whether final mass (log transformed to achieve normality) depended on experimental treatments in a model with all possible interactions among experimental treatments (SAS 8.2, SAS Institute, Cary, NC). Mass data were back transformed for graphical presentation. Single species *ANOVAs* were used to investigate significant interaction terms in the full analysis and Fisher's Least Significant Difference Test was used to test for differences between treatment means (Stat View 5.0, SAS Institute, Cary, North Carolina).

RESULTS

The percent of root mass was independent of all factors other than species ($F_{5,238}=119.80$, $P<.0001$). It was lowest for *Pinus* (29%) followed by *Liquidambar* (40%), *Q. nigra* (46%), *Sapium* (47%), *Nyssa* (53%) and *Q. alba* (73%). The contrasts among species were significant at $\alpha=0.05$ for all pairs of species except *Q. nigra* vs. *Sapium*. Because allocation patterns are independent of treatments (modeled as a percentage of belowground root biomass) and species is the only significant factor explaining the allocation pattern variance, the remainder of the analyses utilized total mass as the dependent variable.

Total mass varied among species (Table 1, Fig. 1) and the contrasts among species were significant at $\alpha=0.05$ for all pairs of species except *Q. alba* vs. *Nyssa* and *Liquidambar* vs. *Q. nigra*. No other main effect significantly affected mass in the *ANCOVA* (Table 1). Total mass depended on starting height in the *ANCOVA* (Table 1). The species which had significant correlations between starting height and log (final mass) in z-tests were *Q. alba* ($r=0.59$, $P<0.0001$) and *Nyssa* ($r=0.41$, $P<0.001$). Variation in mass depended on several interactions: species/noculation, species/fertilization, species/inoculation/fertilization, and species/inoculation/fungicide. Since each interaction term had species as one of the factors, individual species *ANOVAs* were used to help identify the main factors influencing the interactions.

The significant effect of species/inoculation in the full model indicated that species differed in the direction or magnitude of their responses to inoculation. All five native species tended to have lower mass when inoculated but this difference was significant only for *Nyssa* ($P<0.01$) in single species *ANOVAs*. *Sapium* had significantly higher mass when inoculated ($P<0.01$). In a separate analysis with a two-level predictor that indicated whether a species was native vs. *Sapium*, the interaction of this term and inoculation was significant ($P<0.05$).

The significant effect of species/fertilization in the full model indicated that species differed in their responses to fertilization. In single species *ANOVAs*, *Pinus* ($P<0.01$) and *Liquidambar* ($P<0.05$),

Table 1. The dependence of log(final mass) on experimental treatments in an *ANCOVA* with starting height as a covariate. Significant terms are noted with an asterisk (*).

Factor	*df*	SS	F-Value	P-Value
Species*	5	48.2	157.7	<0.0001
Fertilizer	1	0.1	1.6	0.20
Fungicide	1	0.0	0.2	0.70
Inoculum	1	0.1	0.9	0.35
Species/Fertilizer*	5	0.8	2.6	<0.05
Species/Fungicide	5	0.6	1.9	0.10
Species/Inoculum*	5	1.3	4.4	<0.001
Fertilizer/Fungicide	1	0.0	0.3	0.58
Fertilizer/Inoculum	1	0.1	0.9	0.34
Fungicide/Inoculum	1	0.0	0.5	0.48
Species/Fertilizer/Fungicide	5	0.3	0.9	0.50
Species/Fertilizer/Inoculum*	5	0.8	2.7	<0.05
Species/Fungicide/Inoculum*	5	0.8	2.7	<0.05
Fertilizer/Fungicide/Inoculum	1	0.1	1.3	0.26
Species/Fertilizer/Fungicide/Inoculum	5	0.3	0.9	0.45
Starting height*	1	1.2	19.6	<0.0001
Error	238	14.5		

but no other species, were significantly larger when fertilized (Fig. 1). *Pinus* had larger mass in fertilized controls and maintained this increase when inoculated. However, *Liquidambar's* growth had significant mass increases with inoculation in the fertilized treatments only.

Single species *ANOVAs* show that the significant interaction of species/fertilization/inoculation in the full model was related to the idiosyncratic effect of these treatments on *Liquidambar* mass ($P<0.01$, Fig. 1). Inoculation reduced *Liquidambar* mass in low fertility conditions but increased it in high fertility conditions.

The significant effect of species/inoculation/fungicide largely reflected the distinct responses of *Sapium* to fertilizer and fungicide since the interaction of these treatments was only significant for *Sapium* ($P<0.01$) in single species *ANOVAs*. Submodels showed fungicide-non-inoculated plants to be significantly different from fungicide-inoculated plants and contol (non-fungicided, non-inoculated) plants to be significantly different from fungicided-inoculated plants by Fisher's Least Significant Difference Test, respectively ($P<0.01$, $P<0.05$). Specifically, *Sapium* mass was lowest in the fungicide only treatment (average = 7.8 g) followed by control (non-inoculated and non-fungicided), (15.1 g), inoculation only (15.1 g), and finally the combination of inoculation and fungicide (20.9 g).

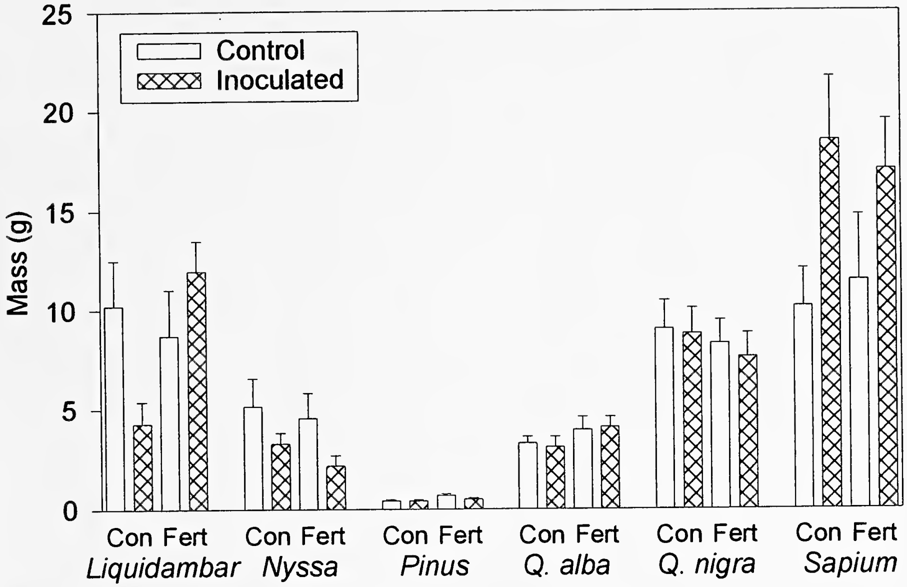

Figure 1. The dependence of mass (g) of *Liquidambar styraciflua*, *Nyssa sylvatica*, *Pinus taeda*, *Quercus alba*, *Quercus nigra*, and *Sapium sebiferum* seedlings on fertilization (con = no fertilizer, fert = fertilized) and mycorrhizal inoculation after 20 weeks. Fungicide treatments are not shown. See Table 1 for statistical results.

DISCUSSION

Sapium's striking positive growth response to mycorrhizal inoculation (65% increase) differed markedly from the neutral to negative responses of native tree species (Fig. 1). The magnitude of reductions in growth of the five native tree species in response to inoculation ranged from negligible (*Q. alba* = 1% reduction, *Q. nigra* = 6%) or minor (*Pinus* = 17%, *Liquidambar* = 24%) to large and significant (*Nyssa* = 46%) but the direction of the response to inoculation was always negative. *Sapium* was clearly able to gain large benefit from mycorrhizal associations with a generalist mycorrhizal inoculum in conditions where natives could not. It appears that natives were unable to benefit from the generalist inoculum in this study suggesting that mycorrhizal specificity is important (Bever 2002; Klironomos 2003). The strains used in this study may not be beneficial in these conditions and may create an unnecessary obligate symbiosis with direct translations to decreases in growth (Hetrick et al. 1988; Hetrick 1991). This supports the hypothesis that unusual relationships between the exotic *Sapium* and North American mycorrhizae species, such as those in the inoculum, may contribute to *Sapium*'s success as an invader.

There are a number of explanations for why lack of specialist mycorrhizae (Bever 2002; Klironomos 2003), which was predicted to be beneficial, appeared to be especially detrimental in fertilized treatments for *Nyssa, Pinus, Q. nigra* and for the native species *Liquidambar* and *Nyssa* in unfertilized treatments in this experiment. First, carbon drain on host plants, which is well documented (Buwalda & Goh 1981; Hetrick 1991; Johnson 1993; Peng et al. 1993; Graham et al. 1996) may have exceeded the benefits of increased nutrients and/or water in these relatively fertile, well-watered greenhouse conditions. Second, mycorrhizae in this experiment may have used carbon from plants largely for respiration rather than increasing extraradical hyphae surface area and increasing nutrient absorption (Peng et al. 1993; Graham et al. 1996). Increases in maintenance respiration, as well as higher root construction costs due to high lipid vesicle allocation, has been shown in P addition experiments for *Citrus volkameriana* (Peng et al. 1993, Graham et al. 1996) and has been attributed to decreases in carbohydrate root exudates from plants in highly fertilized soils (Johnson et al. 1997).

The unexpected results for fungicide and inoculation combinations, in particular the effects on *Sapium* mass, were inconsistent with the expectation that seedlings in the two treatments, non-inoculated fungicide only and inoculation plus fungicide, would be identical in size. This suggests that fungicide applications were not an effective method of fungal control. One possible explanation is that non-spore ingredients in the mycorrhizal inoculum had phytotoxic effects on seedling growth in the presence of fungicide. The reduction of *Sapium* mass by fungicide application (without inoculum) might indicate that beneficial microbes (phosphate-solubilizing microbes and plant growth-promoting bacteria) were present in the potting soil which were killed by the fungicide (Allen 1992). Alternatively, it might indicate direct toxic effects of fungicide on *Sapium*. The recovery of *Sapium* growth with inoculation in fungicide treatments suggests that the mycorrhizal inoculum was not effectively suppressed and that mycorrhizae may be acting synergistically with microbes in the fungicided soil that were not effective or prevalent in the non-fungicided soil. One goal of this greenhouse experiment was to develop methods that could be applied in field experiments. Further work with direct assays of mycorrhizal and non-mycorrhizal fungi in experiments with *Sapium* is needed to complete the identification of reliable field methods and identify the cause of the seemingly anomalous inoculation and fungicide result.

The prediction of decreased response of all species to mycorrhizal inoculation in high fertility environments was based on the assumption that mycorrhizal carbon costs are not offset by the benefits of nutrient gathering in conditions in which nutrients are abundant (Menge et al. 1978; Buwalda & Goh 1981; Hetrick et al. 1988; Hetrick 1991; Johnson 1993; Peng et al. 1993). The positive response of *Liquidambar* to mycorrhizal inoculation only in fertilized conditions was opposite the prediction that the benefit of mycorrhizal associations would be lower in more fertile conditions (Fig. 1). Indeed, the reverse pattern observed here suggests that there may be potential for strong competition for nutrients between mycorrhizae or other soil microbes and plants in low fertility environments that may counteract the potential benefit of mycorrhizal associations in these conditions (Bardgett et al. 2003).

The strong benefit of mycorrhizal inoculation for *Liquidambar* in some conditions (Figure 1) indicates that the competitive advantage *Sapium* might gain from mycorrhizal associations may vary with native species and soil fertility (Marler et al. 1999).

One theory explaining the success of invaders in their introduced range is the Enemy Release Hypothesis. It predicts that invasives experience a release from the pressures of the natural enemies in their native range and can therefore allocate additional resources to growth and reproduction (Alpert et al. 2000; Maron & Vila 2001; Keane & Crawley 2002; Mitchell & Power 2003). However, little attention has been given to belowground enemies. This experiment raises the possibility that the large size of *Sapium* in all conditions, although doing better with inoculum than natives, (Figure 1) reflects presence of belowground pathogenic fungi that more readily attack native tree species.

The results reported here would be more compelling with confirmation of mycorrhizal colonization and dependence by direct examination. Further, it is imperative that these results be verified in field trials as well as in experiments including competitive interactions between species. Such experiments are currently underway to rigorously test the preliminary conclusion presented here that interactions with soil microbes play a role in *Sapium* invasions in east Texas forests.

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CHARACTERIZATION OF ARTHROPOD ASSEMBLAGE SUPPORTED BY THE CHINESE TALLOW TREE (*SAPIUM SEBIFERUM*) IN SOUTHEAST TEXAS

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Abstract.—Arthropod abundance, species richness and trophic structure were measured on the introduced species Chinese Tallow tree (*Sapium sebiferum* (L.) Roxb.) in southeast Texas. Samples were collected using sweep nets between June and October of 2001. A total of 811 individuals and 160 arthropod species were caught. Orders Diptera, Acari, and Araneida were abundant on *Sapium*, while orders such as Thysanoptera, Neuroptera, Orthoptera were present in much lower relative abundances. The order Hemiptera was markedly low in abundance and species richness. Compared to available data on native ecosystems, predators and detritivores were relatively abundant while herbivores and total arthropod diversity were relatively low on *Sapium*. These results suggest that *Sapium* has not yet acquired an insect fauna comparable to native plants in Texas.

Arthropods represent a significant proportion of faunal community diversity and have vital roles in ecosystem functioning (Wilson 1992; Price 1997). A number of ecosystem services are performed by arthropods, such as nutrient recycling, seed dispersal, herbivory, and pollination (Proctor & Yeo 1972; Petrusewicz & Grodzinski 1975; Davidson & Morton 1981; Jones et al. 1994). Introduced plant species have been shown to alter ecosystem functioning, reduce native diversity, and promote extinction of native species (Vitousek 1986; Liebhold et al. 1995; Mack et al. 2000), and through changes in vegetation structure, composition and host quality, they may affect arthropod assemblages. Insect diversity is frequently correlated with the diversity of plants (Schowalter 1995; Siemann 1998) and architectural complexity of a habitat (Strong et al. 1984). When previously diverse habitats are converted to monospecific stands of non-native plants, insect species richness will often be lower.

Factors that influence arthropod colonization rates on introduced plant species may affect subsequent community composition and structure. Strong et al. (1984) suggested that taxonomic, phenological, biochemical, and morphological similarities between introduced and native plants, as well as geographic range, may influence how quickly introduced plants are colonized by native arthropods. However, arthropod host choice is typically driven by physiological and behavioral adaptations in response to host plant quality (Price 1997; Schowalter 2000). Host plants considered low quality for arthropod growth and development, are typically highly defended and/or nutritionally poor (Price et al. 1980). Host choice usually divides herbivorous insects into two categories, generalists and specialists (Feeny 1976). Generalists capitalize on the most abundant and obvious resource, whereas specialists possess increased efficiency but reduced resource choice (Feeny 1976; Brown 1984). Therefore, generalist arthropods are thought to be more commonly found on introduced plant species than native species (Strong et al. 1984; Lankau et al. 2004), but little empirical evidence supports this assertion.

Sapium sebiferum (L.) Roxb. (Euphorbiaceae) also known as *Triadica sebifera,* invades coastal tallgrass prairie, disturbed areas, and intact floodplain forests in east Texas (Bruce et al. 1997). The enemy release hypothesis has been used to explain the success of some introduced species including *Sapium* (Elton 1958; Keane & Crawley 2002; Siemann & Rogers 2003a). It asserts that alien species are introduced without their co-evolved specialist herbivores and pathogens. This release from natural enemies may give alien species a competitive advantage over native plants (Elton 1958; Groves 1989; Lodge 1993; Tilman 1999). Indeed, there is evidence that herbivore loads are lower on introduced plant species than native species (Southwood et al. 1982; Strong et al. 1984; Yela & Lawton 1997). Furthermore, biological control agents can sometimes control alien plant populations (Goeden & Louda 1976; Groves 1989). If the enemies release hypothesis is valid, insects may play an important role in the invasion of *Sapium.*

The objective of this study was to characterize the arthropod community by quantifying arthropod taxonomic richness and abundance on a monospecific stand of *Sapium*, growing on a former coastal prairie in southeast Texas, and comparing to data from native habitats in southeastern Texas (Birch 1975; McFadden 1978; Cameron & Byrant 1999). It was predicted that: (1) fewer herbivore species would be found on *Sapium* than in native communities if *Sapium* is avoided by North American herbivores, and (2) the arthropod community structure on *Sapium* would be different from that found in native habitats, as *Sapium* has been present for a shorter time and is therefore less likely to have acquired a full insect fauna.

MATERIALS AND METHODS

Focal study species.—Originally from Asia, Chinese tallow tree (*Sapium sebiferum*) was introduced to Georgia in the late eighteenth century and subsequently into Texas in the early 1900's (Bruce et al. 1997). *Sapium* is a dominant invasive species in the southeastern United States (Flack & Furlow 1996; Bruce et al 1997). Once established it can form dense monospecific stands with little understory vegetation (Bruce et al. 1997). It experiences low levels of herbivory in Texas (Siemann & Rogers 2001; 2003a; 2003b) but the diversity and composition of associated arthropods in Texas is not known.

Study site.—The study was conducted at the University of Houston Coastal Center (henceforth known as UHCC), a 374 ha research area, located 50 km SE of Houston, Texas. Most of the research site consists of *Sapium* stands in areas that originally would have been tallgrass prairie. This study was conducted in a monospecific *Sapium* stand that was estimated to be 30 years old.

Sampling protocol.—This *Sapium* stand was sampled 16 times between 8 June and 24 October 2001. The sampling frequency was devised for taxa that emerge for only short periods and, or have short life spans. On each sampling occasion, four samples were collected randomly from *Sapium*. Each sample was collected along a 16 m transect. Transects were selected for minimal undergrowth to minimize the influence of other plant species on the focal arthropod community. Each transect was sampled for arthropods using 30 swings of a sweep net (15 inches diameter) that reached 5.8m into the canopy (see Siemann 1998 for comparisons of sampling methods affecting relative abundance and species richness). Sampling was conducted at approximately the same time of day and under similar weather conditions (dry and warm).

Arthropod identification.—Arthropod specimens were sorted under magnification and identified to either species or morphospecies within family or genus, and abundance, and trophic group was recorded by taxon. Individuals from the order Araneida (spiders) were often not identified beyond order due to their taxonomic complexity and lack of a local reference collection. Morphospecies have been shown to correlate with arthropods identified by entomologists (Oliver & Beattie 1996), and this technique is often effectively utilized in the characterization of communities (Ingham & Samways 1996; Siemann 1998; Symstad et al. 2000).

Determination of trophic level.—For each species or morphospecies, a trophic group was determined for the developmental stage at which the individual was caught by referring to relevant literature (Arnett 1960 1993; Borror & White 1970; McAlpine et al. 1981; 1987; Schuh & Slater 1995). The functional groups were the following: herbivore, detritivore, predator, parasite, omnivore, non-feeding, and unknown. Herbivores included any arthropod feeding primarily on living plant material. Omnivores were defined as individuals feeding on plants and animals. The group 'unknown' was assigned for those whose trophic grouping could not be determined through lack of available knowledge or insufficient taxonomic determination. Little is known about feeding habits for some taxonomic groups, especially those without agricultural or medical importance. There are some arthropods that only feed in their larval stage; therefore, a non-feeding group was included.

Data from previous studies.—The native sites and habitats sampled by Cameron & Byrant (1999) were located near Sealy, Texas, approximately 110 km NW of the *Sapium* study site (UHCC). They sampled using a beating net for woody areas and a sweep net in herbaceous vegetation. The beating nets usually have heavier canvas fabric that collects smaller individuals than a sweep net. The habitats included: riparian woodland with ungrazed pasture and savanna woodland (RW1), dense riparian woodland with less open grassland (RW2), bottomland woodland with dense herbaceous understory (BW3), fluvial woodland with open understory with periodic flooding and bordered by pasture (FWP4), dense drier woodland with woody understory (DW5), grazed pasture with a few woody species (GP6), abandoned pasture with patches of riparian woodland (PW7), and coastal prairie with no woody vegetation, surrounded by agriculture and grazing (CP8). Cameron & Byrant (1999) did not include non-insect arthropods in their study so these groups were excluded from the UHCC data (including *Sapium* data) for comparative analyses.

Two studies from UHCC on arthropod communities were also included in this study (Birch 1975; McFadden 1978). Arthropod data from high (HDB) and low densities (LDB) of *Baccharis halimifolia* L. were utilized from an earlier study by Birch (1975). Like *Sapium*, *Baccharis* is both common and woody, yet *Baccharis* is native to the area. Birch (1975) sampled the stands on four occasions in 1975, using a D-vac. Siemann (1998) found that relative richness and abundance values for D-vac and sweep net samples were strongly correlated. McFadden (1978) collected arthropod data in the coastal prairie at

UHCC (UHCP) every two months, a total of seven times in the year, using a sweep net. Sampling effort was standardized for McFadden (1978), Birch (1975), and Cameron & Byrant (1999) by using relative rather than absolute values. Birch (1975) and McFadden (1978) are the only available studies on arthropod communities at the UHCC.

Data analyses.—To assess the differences in the *Sapium* insect community from those in native Texas habitats, a non-metric multidimensional scaling (NMS) ordination was conducted using relative abundance of seven insect orders from *Sapium,* high and low densities of *Baccharis* (Birch 1975), coastal prairie (McFadden 1978), and eight native sites studied by Cameron & Bryant (1999). Araneida and Acari were excluded. NMS is a non-parametric, iterative technique based on ranked distances among sites (McCune & Grace 2002). The number of dimensions was determined by a minimal stress (departure from monotonicity). The distance matrix of sites used for ordination was $1\text{-}D_s$, in which D_s is Sørensen's similarity index. Using the distance matrix output by PC-ORD Version 4, the distance ordination was conducted in SAS V.8 (SAS Institute 2000) with routine PROC NMS.

RESULTS

A total of 811 individuals and 160 species in 15 orders of arthropods were caught in a total of 1920 sweeps. Some orders were abundant on *Sapium*, such as Acari (mites), Araneida (spiders), and Diptera (flies), which accounted for 78% of the individuals in the community (Table 1). The most diverse orders were Diptera (36% species richness) and Acari (13% species richness). Coleoptera (beetles), Homoptera (leafhoppers), Hymenoptera (wasps and ants) and Psocoptera (barklice) were less abundant on *Sapium*. Eight orders were rarely encountered (Collembola (springtails), Dictyoptera (mantids and cockroaches), Ephemeroptera (mayflies), Hemiptera (true bugs), Lepidoptera (moths and butterflies), Neuroptera (lacewings), Orthoptera (grasshoppers and crickets), and Thysanoptera (thrips). Twenty immature individuals were caught, of which 13 were Orthoptera, and the remainder were Coleoptera, Homoptera, and Thysanoptera.

A species accumulation curve was constructed to determine the number of species collected versus sampling effort for the data on *Sapium*. Three saturating equations were fitted to the curve (Tablecurve 2D, Systat, Point Richmond CA). They indicated that the total number of species in the community was 189 (first order intermediate kinetic

Table 1. Abundance and species richness of arthropods by taxonomic order summed over all samples.

Order	Abundance	Species Richness
Acari	165	20
Araneida	248	—
Coleoptera	25	14
Collembola	1	1
Dictyoptera	2	2
Diptera	222	57
Ephemeroptera	1	1
Hemiptera	2	2
Homoptera	36	16
Hymenoptera	39	16
Lepidoptera	4	4
Neuroptera	14	7
Orthoptera	13	6
Psocoptera	36	11
Thysanoptera	3	3
TOTAL	811	160

function), 191 (simple equilibrium, net rate and equilibrium concentration function), or 208 (first order intermediate kinetic function with equilibrium) which suggests the sampling effort on *Sapium* caught 85%, 84%, or 77% of the species respectively. A species-sweep curve constructed by McFadden (1978) showed that 1000 sweeps would contain 85% of the diversity. Cameron & Byrant (1999) also estimated they collected 85% of the diversity (based on McFadden 1978). Birch (1975) did not create a sampling curve.

The most abundant family encountered was Oripodidae (beetle or armored mites), which accounted for 14% of total arthropod community abundance (Table 2). Chironomidae (non-biting midges), Lauxaniidae (Lauxaniid flies), and Dolichopodidae (long legged flies) were also relatively common (Table 2). The most diverse (species rich) among these were Dolichopodidae and Chironomidae. Other common families were Psocidae (common barklice), Sciaridae (dark winged fungus gnats), Formicidae (ants) and Coccidae (scales) (Table 2).

Only two families were encountered that might be considered as specialist herbivores. These were Coccidae (scales) and Cicadellidae (leafhoppers) both in the order Homoptera. Homoptera are often known to stay on host plants where their eggs are laid.

Predators (326 individuals) and detritivores (241 individuals) together represented 70% of the arthropod assemblage supported by *Sapium*. Herbivores were considerably less abundant and composed only 7% of

Table 2. Fifteen most abundant families sampled from *Sapium*. The families listed account for 53% of total arthropod community abundance and 55% of total species richness.

Order	Family	Abundance	Species Richness
Acari	Oripodidae	115	5
Diptera	Chironomidae	61	12
Diptera	Lauxaniidae	60	9
Diptera	Dolichopodidae	53	13
Psocoptera	Psocidae	25	6
Diptera	Sciaridae	18	8
Hymenoptera	Formicidae	16	4
Homoptera	Coccidae	14	5
Homoptera	Cicadellidae	11	5
Hymenoptera	Braconidae	11	3
Diptera	Chloropidae	10	6
Orthoptera	Gryllidae	9	4
Neuroptera	Chrysopidae	8	3
Psocoptera	Pseudocaeciliidae	8	3
Coleoptera	Coccinellidae	7	2

all *Sapium* community arthropods (58 individuals). Insect relative abundance for the additional trophic categories were 3% for omnivores and parasites, 10% unknown, and 8% non-feeding on *Sapium*. However, species richness was more evenly proportioned among the trophic categories. Detritivores were the most species rich (43 species or morphospecies) but only represented 27% of the community diversity. Both herbivores and predators had similar levels of diversity, representing 20% and 17% respectively.

The arthropod community on *Sapium* differed from the communities found on native sites sampled by Birch (1975), McFadden (1978), and Cameron & Byrant (1999) (Table 3). After Acari and Araneida data were removed, relative species richness and abundance were recalculated to make all the data sets comparable. The relative richness of herbivores (29%) was approximately 50% less on *Sapium* than on native vegetation (native herbivore range 49-67%). In contrast, both predator and detritivore relative richness was higher on *Sapium* (24% and 38% respectively) than the native site averages (12% and 16% respectively). The average relative species richness for predators from native sites was 12% (range 6-19%), and the average for detritivores (native sites) was 16% (range 7-24%). Parasites on *Sapium* were similar in their relative species richness (9%) compared to the native sites (range 8-21%). Cameron & Byrant (1999) did not present results on the trophic distribution of arthropod abundance.

Table 3. Arthropod relative species richness by trophic group for *Sapium* samples in this study ("*Sapium*") and habitats sampled by Birch (1975), McFadden (1978), and Cameron & Byrant (1999). Refer to methods for description of sites.

Sites	Herbivore %	Predator %	Parasite %	Detritivore %
RW1	57	9	15	20
RW2	57	7	11	24
BW3	55	12	16	17
FWP4	61	11	12	17
DW5	59	11	9	21
GP6	58	6	14	22
PW7	67	8	10	15
CP8	54	13	16	16
UHCC prairie	67	19	8	7
HD *Baccharis*	56	10	21	12
LD *Baccharis*	49	14	21	16
Sapium	29	24	9	38

The comparison of community composition of *Sapium* and native sites sampled by Birch (1975), McFadden (1978), and Cameron & Byrant (1999) showed both differences and similarities in the relative abundance of orders (Table 4). Arthropod relative abundance on *Sapium* was comparable within the range of relative abundance at native sites for Homoptera, Coleoptera, Orthoptera, Hymenoptera, and Lepidoptera (Table 4). However the relative abundance found on *Sapium* was higher for Diptera and 'others', and lower for Hemiptera (Table 4).

The NMS ordination of relative abundance of orders indicated that the insect community on *Sapium* differed substantially from that of native sites (Figure 1). A 3-dimensional solution was found. However, a two dimensional graph is presented, for ease of interpretation (Figure 1). A total of 38 iterations were run for the final solution, and the final stress was 0.08196. A final stress value between 0.1 and 0.05 is generally interpreted as a good ordination with negligible risk of inferring false conclusions (McCune & Grace 2002). The UHCC sites were distinctly separated from Cameron & Byrant's (1999) sites along dimension 1 (Figure 1). The *Sapium* site was located at the extremes of both axes (Figure 1). The grazed pasture site (GP6) was the most similar native site to *Sapium* in insect community (Sørenson's similarity index (SSI) = 0.75), followed by UHCC coastal prairie (UHCP) (SSI = 0.56), while abandoned pasture with patches of riparian woodland (PW7) was the most different (SSI = 0.31).

Table 4. Relative abundance of insects (Acari and Araneida excluded) by order from the native habitats sampled by Birch (1975), McFadden (1978), Cameron & Byrant (1999), and for *Sapium* samples in this study. These values are the percentage of each order within each site. 'Others' include all other orders not already listed. Refer to methods for site abbreviations. HOM=Homoptera, HEM=Hemiptera, COL=Coleoptera, ORT=Orthoptera, DIP=Diptera, HYM=Hymenoptera, LEP=Lepidoptera.

Sites	HOM	HEM	COL	ORT	DIP	HYM	LEP	Others
RW1	13.2	39.0	33.1	3.6	6.9	3.8	0.3	0.4
RW2	29.8	11.6	14.6	26.0	11.8	5.1	1.0	0.0
BW3	23.0	8.7	47.3	7.5	8.3	4.3	0.6	0.3
FWP4	12.0	2.7	66.3	7.6	7.0	4.1	0.1	0.5
DW5	20.0	18.8	21.0	10.0	25.0	4.0	1.0	1.0
GP6	12.1	16.4	6.9	11.9	49.5	3.2	0.0	0.0
PW7	28.1	1.8	23.5	37.6	5.7	2.9	0.3	0.1
CP8	4.0	38.7	6.2	23.2	21.7	6.2	0.3	0.1
UHCC prairie	15.7	14.1	20.1	4.4	20.0	20.7	1.6	3.2
HD *Baccharis*	34.0	19.3	3.9	0.3	9.7	31.8	0.5	0.5
LD *Baccharis*	17.8	39.7	1.9	0.0	11.6	23.4	1.0	4.7
Sapium	9.0	0.5	6.3	3.3	55.8	9.8	1.0	14.3

DISCUSSION

Consistent with the enemies release hypothesis, *Sapium* woodlands in southeastern Texas supported communities depauperate in herbivores and specialists, and were instead composed primarily of predators and detritivores (Table 1, Table 3). These data support earlier predictions of fewer herbivores and a differing arthropod community structure on *Sapium* compared to native habitats. The differences in arthropod abundance and species richness between *Sapium* woodlands and native habitats were substantial (Figure 1, Table 3). Nevertheless, *Sapium* may be in the early stages of acquiring a more typical insect assemblage. Other work has shown that introduced plants may take up to 300 years to support an insect fauna indistinguishable from native plants (Strong 1974; Strong et al. 1984). Therefore the difference in the fauna documented on *Sapium* might be consistent with only 100 years of colonization time in Texas.

A large proportion of the species or morphospecies were infrequently encountered on *Sapium*, suggesting either a high number of transient individuals or rare individuals. This is considered typical in arthropod communities (Siemann et al. 1999).

The differences in arthropod communities between *Sapium* woodlands and native habitats might reflect unusual taxonomic, phenological,

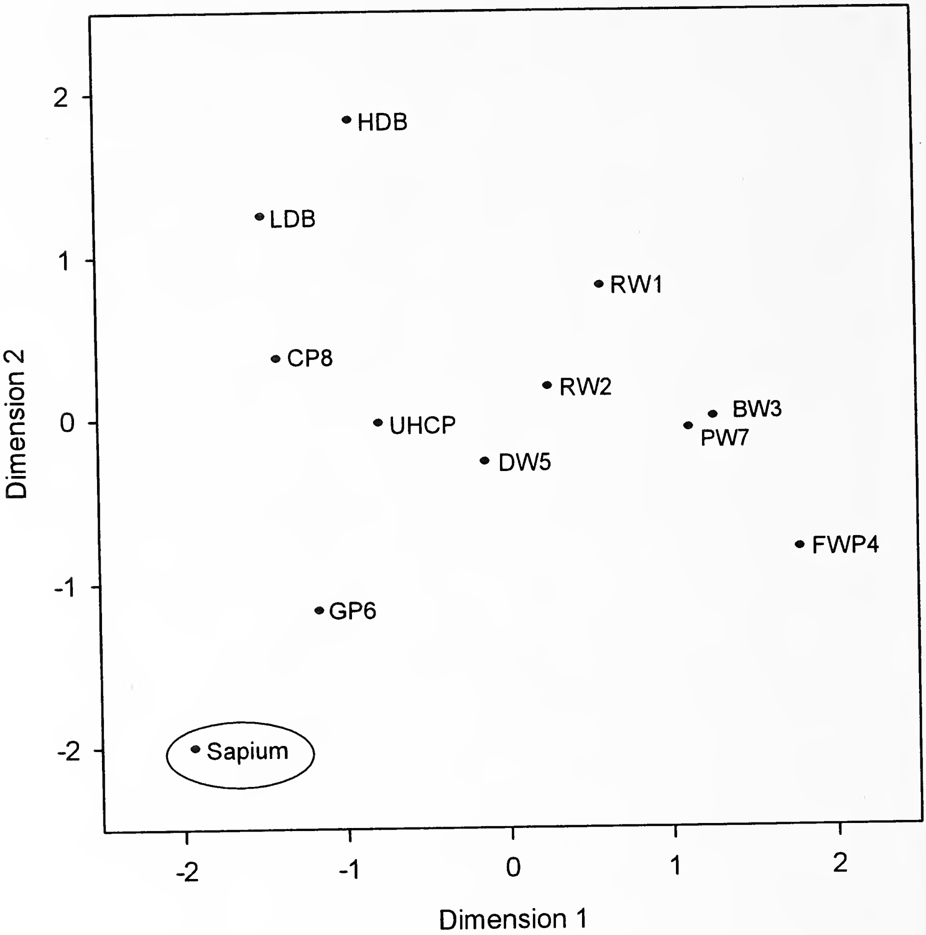

Figure 1. Non-metric multi dimensional scaling ordination of the relative abundance of the seven major insect orders (see Table 4) sampled from *Sapium*, UHCC coastal prairie (McFadden 1978), high and low densities of *Baccharis* (Birch 1975), and the eight native habitats from Cameron & Byrant (1999). Refer to methods for site abbreviations.

biochemical, and morphological properties of the exotic species (Strong et al. 1984). Taxonomically, there are no other native tree species belonging to the Euphorbiaceace family, although there are a number of herbs such as *Euphorbia bicolor* (snow-on-the-prairie) and *Croton capitatus* (woolly croton). However, phenologically and morphologically it is similar to the native mid-sized, broad-leaved deciduous trees, such as *Celtis laevigata* (Bush & Van Auken 1986; Bruce et al. 1997), suggesting that *Sapium* is not unusual in this regard. *Sapium*'s ability to form dense monospecific stands and reduce habitat complexity in the understory is unprecedented in this region, thus simple plant architecture and or low local plant diversity might account for reduced arthropod diversity and abundance.

Of all the native habitats examined, the grazed pasture site was most similar in arthropod composition to *Sapium* woodlands (Figure 1, Table 4). Both *Sapium* and grazed pasture are unnatural types of habitat. Originally the *Sapium* sampling location would have been coastal tallgrass prairie approximately 100 years ago, although 90 hectares of coastal prairie has now been restored. The UHCC coastal prairie site (McFadden 1978) was the second most similar native site, while the coastal prairie (Cameron & Byrant 1999) was the fourth most similar. *Sapium* woodlands may have recruited some arthropods from adjacent prairie habitat, and this may account for some degree of similarity between the arthropod community composition of *Sapium* and native coastal prairie sites sampled by McFadden (1978) and Cameron & Bryant (1999).

Comparisons to Birch (1975), McFadden (1978), and Cameron & Byrant (1999) are informative. However, there are differences between the approaches that should be noted (also see methods). First, sampling was conducted at different times and years. Birch (1975), McFadden (1978), and Cameron & Byrant (1999) all sampled in the mid to late 1970's, although there have been no significant, sudden, or large scale changes (such as land use change) in the UHCC vicinity. Furthermore Cameron & Byrant (1999) only sampled in the spring. Generally, insect communities increase in abundance at the beginning of the growing season and decrease at the end of the growing season, yet many populations display substantial fluctuations. *Sapium* arthropod data (total abundance and species richness) exhibited no significant pattern of variation among the sampling periods. Secondly, sampling efforts could differ, but are difficult to quantify or compare. Thirdly, Birch (1975) also used a D-vac in addition to a sweep net (see Siemann 1998). Although there are differences in approaches, the overall relative results should not be greatly influenced by them, especially considering that both McFadden (1978) and Cameron & Byrant (1999) state they collected 85% of the diversity, which is comparable with the *Sapium* data (77-84%). This would suggest that their results are representative of the communities they sampled. Finally, the authors determined trophic data for McFadden (1978) from an appendix of the most common 95 species and morphospecies (from a total of 535). It was assumed that the complete data would have been driven by the most abundant species and morphospecies and so the trophic data determined would reflect this. These factors may have influenced the contrast between the insects found on *Sapium* and in native habitats, but the data indicate a paucity of herbivores found on *Sapium.*

In conclusion, *Sapium* woodlands seem to presently support an atypical arthropod fauna, with Diptera (flies), Acari (mites) and Araneida (spiders) as the dominant orders. *Sapium*'s fauna is mostly composed of predators and detritivores with very few herbivores. The apparent relative lack of a herbivorous food chain supports the prediction and may have important implications in ecosystem functioning. Although *Sapium* woodlands in southeastern Texas appear to have acquired few herbivores in the 100 years it has been present, it is expected that arthropod diversity and possibly abundance will continue to increase on *Sapium* and the composition of associated arthropod fauna will change to be more similar to native communities over time. Perhaps the accumulation of a more robust herbivore fauna will limit *Sapium's* success as an invader in the future.

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TEXAS J. SCI. 56(4):383-394 NOVEMBER, 2004

DIEL ACTIVITY PATTERNS OF THE LOUISIANA PINE SNAKE (*PITUOPHIS RUTHVENI*) IN EASTERN TEXAS

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Abstract.—This study examined the diel activity patterns of six Louisiana pine snakes in eastern Texas using radio-telemetry. Snakes were monitored for 44 days on two study areas from May to October 1996. Louisiana pine snakes were primarily diurnal with moderate crepuscular activity, spending the night within pocket gopher burrows or inactive on the surface. During daylight hours, snakes spent approximately 59% of their time underground within gopher burrows, burned out/rotten stumps, or nine-banded armadillo (*Dasypus novemcinctus*) burrows. Remaining time was spent on the surface either close to subterranean refuge, or in long distance movements that generally terminated at another pocket gopher burrow system. Long distance movements occurred on 45% of the days snakes were monitored and averaged 163 m/movement. When snakes were active, movements related to ambientair temperature; 82% of these movements occurred between 1000 and 1800 hours. These results confirm that Louisiana pine snakes are diurnal and closely associated with Baird's pocket gophers and their burrow systems, and have provided new insight on the ecology of this rare snake.

The Louisiana pine snake (*Pituophis ruthveni*), first described by Stull (1929), is a large-bodied constrictor of the family Colubridae and until recently was considered one of 15 subspecies of *Pituophis melanoleucus* (see Sweet & Parker 1990; Collins 1991; Crother et al. 2003). The Louisiana pine snake is allopatric to other *Pituophis* and its distribution is primarily restricted to the longleaf pine (*Pinus palustris*) ecosystem of west-central Louisiana and eastern Texas (Conant 1956; Reichling 1995). The longleaf pine ecosystem is perpetuated by frequent fire (Platt et al. 1988; Frost 1993). Louisiana pine snakes are semi-fossorial and are closely associated with Baird's pocket gopher (*Geomys breviceps*) burrow systems (Rudolph & Burgdorf 1997). Baird's pocket gophers are the predominant prey of Louisiana pine snakes and their burrow systems are used for foraging, shelter, escape from frequent fires, and hibernation (Rudolph et al. 1998; 2003).

Many have reported on the apparent rarity of *P. ruthveni*; this can be partly attributed to its semi-fossorial habits and secretive nature (Conant 1956; Young & Vandeventer 1988; Rudolph & Burgdorf 1997). Only 57 records of *P. ruthveni* were available through 1990 (Conant 1956; Jennings & Fritts 1983; Young & Vandeventer 1988; Reichling 1989). As a result, this species is considered to be one of the rarest snakes in North America (Thomas et al. 1991). Extreme rarity has prevented researchers from collecting substantial ecological and natural history data on the species and accounts for the paucity of available literature.

In 1993, the USDA Forest Service Southern Research Station initiated a long term study of home range and habitat use of free ranging Louisiana pine snakes in eastern Texas and west-central Louisiana through the use of radio-telemetry. This portion of the study was conducted from May through October 1996 to elucidate diel activity patterns of this snake in eastern Texas.

STUDY AREAS

Two areas were used to monitor Louisiana pine snakes in eastern Texas. Foxhunter's Hill is a 500 ha longleaf pine savanna located on the Sabine National Forest approximately 25.5 km south of Hemphill, Texas, in Sabine County. The second area, Scrappin' Valley, owned by Temple-Inland Forest Products Corporation, is approximately 29 km south of Hemphill, Texas, in Newton County. The portion of Scrappin' Valley used as the study area is a 450 ha longleaf pine savanna. Characteristics common to both sites are: soils with high sand content; diverse herbaceous flora dominated by little bluestem (*Schizachyrium scoparium*) and bracken fern (*Pteridium aquilinum*); over story dominated by longleaf pine (*Pinus palustris*), sparsely distributed blackjack oak (*Quercus marilandica*) and blue jack oak (*Quercus incana*); and areas of encroachment by sweet gum (*Liquidambar styraciflua*), sassafras (*Sassafras albidum*), and yaupon (*Ilex vomitoria*) as a result of past fire suppression. Foxhunter's Hill possesses moderate topographic relief, average basal area of 9 m^2/ha, and heavy leaf litter accumulation and was burned by prescription in late winter of 1993. Scrappin' Valley has lower topographic relief than Foxhunter's Hill, average basal area of 6 m^2/ha, moderate leaf litter accumulation, and was burned in late winter of 1995. Generally, Scrappin' Valley was burned annually while Foxhunter's Hill was burned every 3-5 years, resulting in differential leaf litter accumulation in the two areas.

MATERIALS AND METHODS

Transmitter implantation.—Louisiana pine snakes were captured on the study areas by hand or in drift fence/funnel traps. Temperature sensitive transmitters (Holohil Systems Ltd., SI-2T) 29mm long and 10 mm in diameter with 28 cm whip antennae were implanted subcutaneously following the general procedure of Weatherhead & Anderka (1984). Transmitter life-span was approximately 18 months and maximum transmission range was approximately 1200 m.

Radio-telemetry/data collection.—Snakes were located early in the morning before they became active and emerged from subterranean shelter. A Trimble GPS Professional unit and data logger was used to record each snake's location. Air temperature at the snake's location was measured with a mercury thermometer 0.5 m above the ground in the shade. Substrate temperature was recorded in one of two ways: if the snake was aboveground, the thermometer was placed on the substrate as close as possible to the snake without disturbing it; if below ground, the thermometer was inserted approximately 5 cm into the soil. Snake body temperature was determined by comparison of transmitter pulse rate with a calibration curve for each transmitter.

Throughout the day until sunset, transmitter pulse counts and air temperatures were recorded at 30-45 minute intervals. When the pulse count of a transmitter changed by becoming much slower or faster, indicating a temperature change of the implanted transmitter, the snake was relocated to determine if snake activity had occurred. Six snakes, three on Foxhunter's Hill, and three on Scrappin' Valley were monitored from dawn to dusk for a total of 44 snake days. Movements were recorded and calculated only if an individual moved more than 10 m from its previous location on a given day (Slip & Shine 1988). Movements on six additional days were recorded during the course of other data collection and were also available. Movement distances were calculated through the use of Trimble GPS Pathfinder Office software (Trimble Mapping and GIS Systems Division, Sunnyvale, CA).

Periodic night checks were conducted by locating snakes at sunset and again at midnight and before sunrise to determine if the snakes were active nocturnally. Additional data regarding movement and choice of underground refugia were collected from these and other snakes in addition to the 44 snake monitoring days.

Habitat measurements were taken at each snake relocation point as required for various aspects of research on *P. ruthveni*. Additional habitat measurements were taken at 100 stratified random points determined by overlaying a grid on the overall study site and using the intersections of the grid lines as the random points. The only habitat measurement relevant to this study was the number of burrows counted within an 11.2 m radius (0.04 ha) of each habitat point. *Geomys breviceps* "burrows" were counted as the number of visible push-up mounds and all other burrows were enumerated by the number of actual openings at or near the soil surface.

Data analysis.—Distance moved per snake each day was tested by a Mann-Whitney U-test. Chi-square contingency tests were used to evaluate the time each snake utilized above ground and below ground environments, movement frequency, and refuge/shelter types used. Frequency of movements during 12 two-hour time periods were evaluated by Chi-square contingency tests and all statistical analyses were performed at an alpha level of 0.05.

RESULTS

Six *P. ruthveni* (5 F, 1 M) were monitored during all or most of a total of 44 snake days between July and October, 1996. During the 44 snake days of monitoring, individual snakes were located at the surface between sunrise and sunset for 145 hrs of a total of 354 hrs (41%). The remainder of their time was spent underground in *G. breviceps* burrows, nine-banded armadillo burrows, and decayed or burned stump holes and associated root channels.

In order to determine nocturnal behavior, the six *P. ruthveni* were monitored at approximately sunset, midnight, and sunrise for a total of 20 snake days during July and August. With one exception, all snakes were located below ground in *G. breviceps* burrows each night (n = 17). The exception, a female, was located on the surface beneath dense herbaceous vegetation at sunset on three separate days and remained in that location until the next morning. One of these instances was during pre-ecdysis. For the 44 snake days when extensive monitoring occurred, snakes were assumed to have spent the previous night in *G. breviceps* burrows, based on early morning detections, a total of 29 times. These same snakes were assumed to have spent the succeeding night in subterranean retreats in 38 instances (35 in *G. breviceps* burrows, three in *D. novemcintus* burrows) based on detections at dusk. Data are not available for the remaining 21 nights.

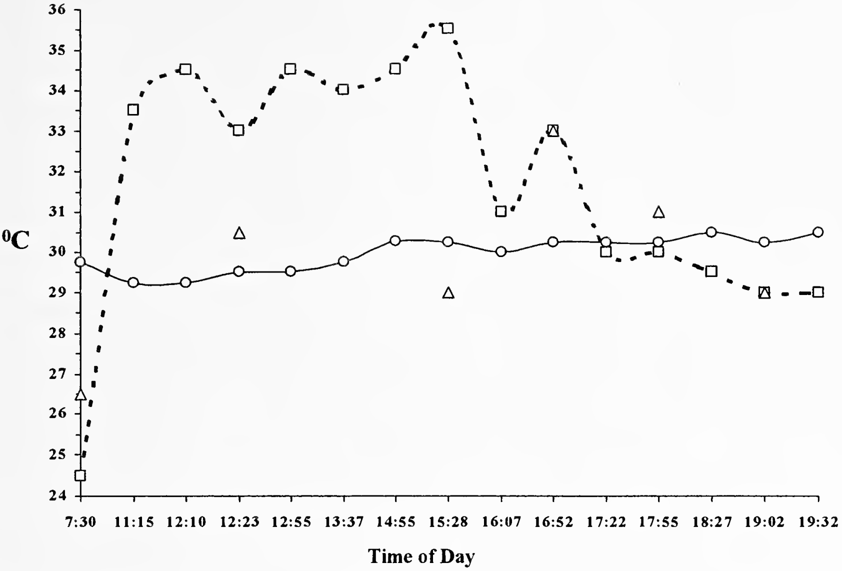

Figure 1. Body temperature (open circles), air temperature (open squares), and substrate temperature (open triangles) for a Louisiana pine snake (*Pituophis ruthveni*) spending daylight hours underground in a Baird's pocket gopher (*Geomys breviceps*) burrow. Adult female 143 on 14 July 1996.

Pituophis ruthveni monitored for daily activity during this study evinced three general daily activity patterns. In 17 cases, snakes remained in *G. breviceps* burrow systems for the entire daily tracking period (Fig. 1). All six snakes except one female from Scrappin' Valley spent at least one entire day in a *G. breviceps* burrow. Conversely, three individuals spent an entire day on the surface. Two of these individuals moved significant distances (225 m and 59 m), and the third was in pre-ecdysis condition with clouded eyes.

In 24 cases various combinations of time were spent on the surface and below ground. These cases were usually associated with substantial surface movement (19 of 24), usually culminating with entrance into another underground refuge (22 of 24) (Fig. 2). Of these 24 snake days, 12 involved snakes that were on the surface when first located in the morning and 12 were in *G. breviceps* burrow systems from which they subsequently emerged. It is unclear if the snakes initially located on the surface had emerged from underground refugia early or had spent the night on the surface, although sampling for nocturnal activity suggests the former in most instances.

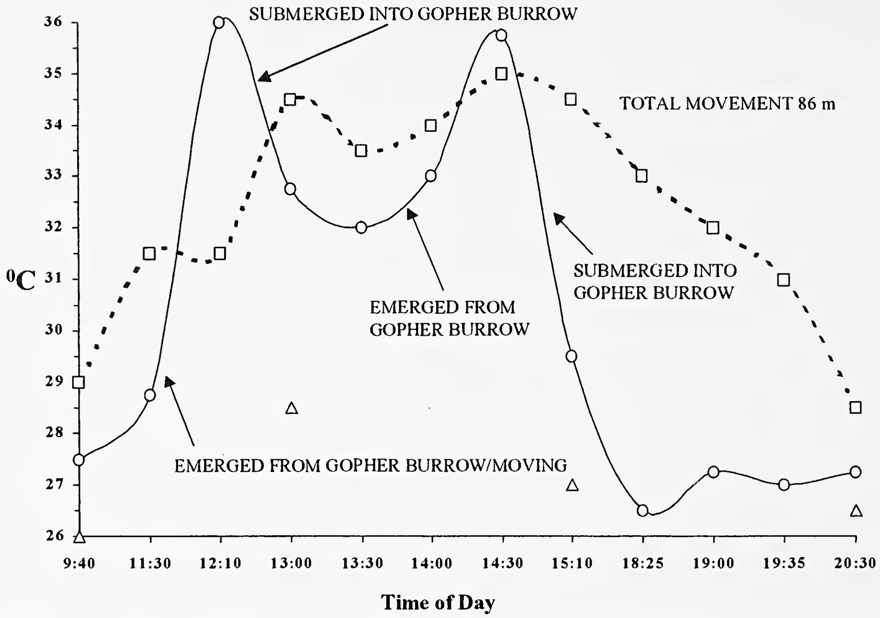

Figure 2. Body temperature (open circles), air temperature (open squares), and substrate temperature (open triangles) for a Louisiana pine snake (*Pituophis ruthveni*) spending portions of a day underground in a Baird's pocket gopher (*Geomys breviceps*) burrow and portions above ground. Adult female 118 on 03 August 1996.

On the 27 snake days in which at least a portion of the day was spent on the surface plus six additional snake days for which movement distances are available, seven snakes remained in the same location, exhibiting only minor movements of < 10 m throughout the day. One individual moved 72 m from its initial location, but returned to its initial location by dusk. In 25 instances snakes moved substantial distances (> 10 m) during the day and were located an average of 163 m (range 11-625 m) from their initial location. Movements occurred from shortly after sunrise until dusk with the majority (82%) between 10:00 and 18:00 hours (Fig. 3). Overall, snakes moved a substantial distance on 20 of 44 days monitored (45.5%). There was a significant difference in frequency of movement between Scrappin' Valley and Foxhunter's Hill snakes ($\chi 2 = 9.99$, $df = 1$, $P < 0.005$) with the Scrappin' Valley snakes moving more frequently (Table 1). Daily movement distances were calculated by summing straight line measurements between consecutive locations and should be interpreted as an underestimation since snakes rarely travel in a straight line (Secor 1994). On days when movement occurred, snakes at Scrappin' Valley (Table 1) moved greater distances, ($\bar{x} = 189$ m, $n = 19$) than did those on Foxhunter's Hill ($\bar{x}$

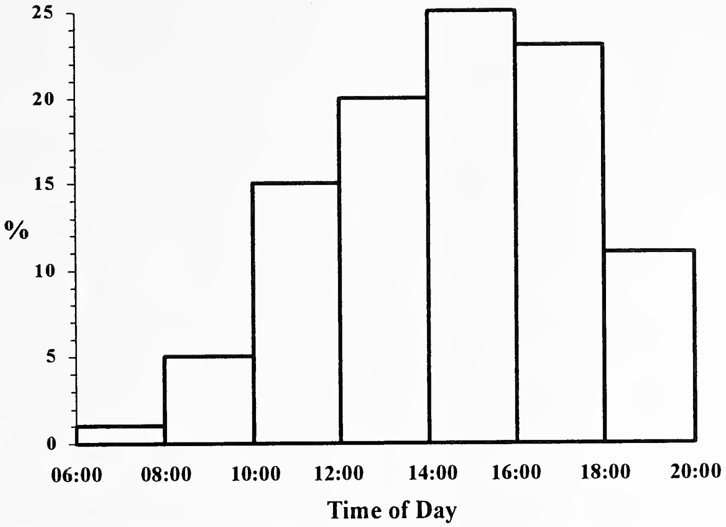

Figure 3. Frequency distribution (%) of movements by six Louisiana pine snakes (*Pituophis ruthveni*) relative to time of day. Data for 12 May - 27 October 1996.

= 91 m, $n = 7$); this difference was significant ($U = 40.5$, $df = 26$, $P < 0.05$).

Pine snake use of underground refugia was recorded on 44 days during which daily activity patterns were monitored and on other days when snakes were located for home range computation. Snakes used *G. breviceps* burrows (80.9%), decayed or burned stumps (15.4%), or *D. novemcintus* burrows (3.7%) as underground refugia. Based on habitat data collected at random points (Table 2), Scrappin' Valley had significantly higher densities of *G. breviceps* burrows ($\chi^2 = 193.9$, $df = 1$, $P < 0.005$) and other types of retreats ($\chi^2 = 10.2$, $df = 1$, $P < 0.005$) than Foxhunter's Hill. Compared to snakes at Foxhunter's Hill, snakes at Scrappin' Valley used underground retreats other than pocket gopher burrows more frequently ($\chi2 = 29.31$, $df = 1$, $P < 0.001$).

The percent of time an individual utilized underground environments on days snakes were monitored was determined through visual observations and making inferences from temperature relationships based on the snakes' body temperature compared to air and substrate temperatures. Snakes at Scrappin' Valley (Table 1) spent a significantly lower proportion of daylight hours underground (45%) compared to snakes at Foxhunter's Hill (74%) ($\chi^2 = 19.96$, $df = 1$, $P<0.05$).

Table 1. Distance moved, movement frequency, and time spent below ground (% time sunrise to sunset) for six Louisiana pine snakes (*Pituophis ruthveni*) at Scrappin' Valley and Foxhunter's Hill in eastern Texas.

Study Area	Range of movement (m)	Mean distance moved per day (m)	Movement frequency (%)	% Time below ground
Scrappin Valley	12-625	189±35	68	45
Foxhunter's Hill	11-184	91±22	24	74
Combined	11-625	163±32	46	59

Table 2. Indices of burrow abundance at snake relocation points and random points (0.04 ha plot) (Scrappin' Valley and Foxhunter's Hill in eastern Texas).

Study Area	No. of gopher burrows at snake relocation points	No. of gopher burrows at random points	No. of burrows at snake relocation points	No. of burrows at random points
Scrappin Valley	7.74	2.52	1.28	0.70
Foxhunter's Hill	8.08	0.64	0.62	0.37

During the May through October period when *P. ruthveni* temperatures were monitored, subterranean retreats, primarily *G. breviceps* burrows, provided a refuge from extreme temperatures. *Pituophis ruthveni* emerged from subterranean retreats at body temperatures ranging from 19 to 29°C. The lower temperatures were recorded in May and October, and the higher temperatures were presumably associated with snakes that were re-emerging within a day or had undergone a period of basking at the burrow entrance prior to actual emergence. Body temperatures of snakes in subterranean retreats were generally within 2°C of soil temperatures at a depth of 5 cm which ranged between 20.75 and 32.5°C.

Body temperatures of snakes present on the surface ranged from 20 to 36.75°C. However, snakes frequently maintained body temperatures between 25.5 and 34.5°C by basking, even when air temperatures were as low as 22°C. Air temperatures never exceeded 35.5°C during monitoring periods, but *P. ruthveni* frequently moved into subterranean retreats as air temperatures approached 35°C.

DISCUSSION

Surface activity of *P. ruthveni* was determined to be essentially diurnal. Individuals were typically located in subterranean retreats, generally those of *G. breviceps,* at night. Snakes located above ground at night were inactive and sheltered under low vegetation. Diurnally, *P. ruthveni* were located above ground 41% of the time, and all recorded movements occurred during daytime. Diurnal activity is typical of *Pituophis* sp. with the exception of populations located in desert environments where diurnal activity is severely limited by high temperatures (Gibbons & Semlitsch 1987). *Pituophis ruthveni* also spent a substantial portion of daylight hours underground (59%), generally in burrows of *G. breviceps*. The close association of *P. ruthveni* with *G. breviceps* burrows provides substantial opportunity to avoid extreme air temperatures.

The close association with the burrows of *G. breviceps* is consistent with other observations of the ecology of *P. ruthveni*. *Geomys breviceps* is the primary prey of *P. ruthveni* (Rudolph et al. 2003), and decline or loss of *G. breviceps* populations, generally resulting from alteration of the fire regime, is hypothesized to be an important cause of population declines (Rudolph & Burgdorf 1997). In addition, *G. breviceps* burrows are the only documented hibernaculum sites, and are used for escape from predators and fire (Rudolph et al. 1998).

Pituophis ruthveni were relatively immobile (i.e., moved <10 m) on 54.5% of days monitored. This is consistent with a figure of 43% for northern pine snakes, *P. melanoleucus melanoleucus*, in New Jersey (Burger & Zappalorti 1989). Relative inactivity has been hypothesized to be a critical component of the thermal ecology of reptiles (Gans & Dawson 1976). This may be the case with *P. ruthveni* because remaining immobile near a subterranean retreat provides immediate access to two divergent thermal regimes. Huey (1982) also suggested that inactivity conserves energy and reduces the risk of predation. In a generally more mobile and active species, *Coluber constrictor*, Plummer & Congdon (1994) found that 90% of inactivity was associated with ecdysis. In *P. ruthveni*, only 13% of inactive days were associated with ecdysis, suggesting that the previously mentioned factors may be involved in the relative inactivity of this species.

Pituophis ruthveni moved an average of 163 m/d on those days when substantial movements were undertaken. This is similar to the findings of Fitch & Shirer (1971) for *P. catenifer* in Kansas (142 m/d) and considerably greater than Parker & Brown (1980) found for *P. catenifer deserticola* in Utah (71 m/d). Long-distance movements in *P. ruthveni* generally involved movement from one *G. breviceps* burrow system to another and consequently reflect the dispersed distribution of these burrow systems.

Pituophis ruthveni, during this and associated studies were found to move very little while underground in *G. breviceps* burrows, typically remaining near the point of entrance in the relatively shallow foraging tunnels. This suggests that *P. ruthveni* behave as sit-and-wait predators when hunting pocket gophers, rather than actively searching within the burrow system. *Geomys breviceps* maintain an intricate burrow complex that can reach 180 m in length (Schmidly 1983), and they can rapidly construct an earthen plug effectively limiting movement by *P. ruthveni* (Rudolph et al. 2003). These observations suggest that a sit-and-wait strategy combined with a brief pursuit may be the most effective strategy to capture *G. breviceps*.

Pituophis ruthveni behavior differed significantly, based on three criteria, between the Scrappin' Valley and Foxhunter's Hill study sites. Snakes at Scrappin' Valley moved more frequently, moved greater distances, and spent less time underground compared to snakes at Foxhunter's Hill. The Scrappin' Valley site was also characterized by a greater density of both *G. breviceps* burrows and other types of retreats compared to the Foxhunter's Hill site. It is possible that the greater availability of subterranean retreats at Scrappin' Valley resulted in fewer restrictions on above ground activity by *P. ruthveni*. The greater availability of *G. breviceps* burrows and other subterranean retreats (primarily burned stump and root channels) is presumably related to the more frequent prescribed fire regime at the Scrappin' Valley site.

The use of subterranean retreats during the active period of the year provided *P. ruthveni* with predictable escape from excessively high air temperatures. Conversely, snakes also had direct access to basking opportunities on the surface that allowed the snakes to maintain a higher body temperature during substantial periods. This general pattern is similar to the results of Himes et al. (2002) for this species in northern Louisiana.

The diel activity budget of *P. ruthveni* reveals a species that is diurnal and semifossorial as is generally typical of other members of the genus in the United States (Fitch & Shirer 1971; Parker & Brown 1980; Sweet & Parker 1990). The importance of burrows of Baird's pocket gophers when combined with previous data and observations (Rudolph &

Burgdorf 1997; Rudolph et al. 1998; 2003) supports the hypothesis that *P. ruthveni* is dependent on *G. breviceps* and ultimately on a frequent fire regime that maintains the herbaceous vegetation that supports *G. breviceps* populations.

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ARBOREAL BEHAVIOR IN THE TIMBER RATTLESNAKE, *CROTALUS HORRIDUS*, IN EASTERN TEXAS

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Abstract.—There have been several recent reports, and anecdotal observations extending back at least to J. J. Audubon, suggesting that the timber rattlesnake (*Crotalus horridus*) is one of the most arboreal members of the genus. Most previous records are of snakes located at heights of less than 5 m. Telemetry studies in eastern Texas have documented more frequent arboreal activity (16.1% of locations of sub-adult snakes) and at greater heights (up to 14.5 m) than previously reported. Unlike previous reports, observations of arboreal activity were restricted to sub-adult snakes (<90 cm SVL), possibly because adult snakes in the current study area are considerably larger than those in other areas where arboreal activity has been documented. Increasing body size and mass may preclude arboreal behavior in larger individuals of this species. Despite considerable speculation on the motivation(s) for arboreal activity in this species, the factors involved remain unclear.

Arboreal behavior in snakes is increasingly recognized as an important aspect of snake ecology (Lillywhite & Henderson 1993). Anecdotal accounts of arboreal activity by timber rattlesnakes (*Crotalus horridus*) date back at least to Audubon (Klauber 1972). In a well known painting by Audubon a timber rattlesnake is depicted attacking Northern Mockingbirds (*Mimus polyglottos*) in a shrub. This painting has elicited considerable discussion concerning the arboreal proclivities of timber rattlesnakes (Klauber 1972).

In recent years, increasing use of radio-telemetry to investigate the biology of timber rattlesnakes has resulted in a proliferation of reports and citations of arboreal activity (Saenz et al. 1996; Coupe 2001; Fogel et al. 2002, Sealy 2002, Bartz & Sajdak 2004). During an ongoing study of *C. horridus* in eastern Texas, Saenz et al. (1996) reported several observations of arboreal behavior. Observations subsequent to the Saenz et al. (1996) report suggest that arboreal behavior, at least by sub-adult individuals, is more frequent in eastern Texas and involves greater heights than previously reported.

A detailed understanding of arboreal behavior in *C. horridus* is limited by the paucity of published records. Saenz et al. (1996) suggested that increasing snake size may limit arboreal behavior in *C. horridus*. Other authors have suggested that arboreal behavior may be related to basking, avoiding flood waters, ecdysis and foraging (Klauber 1972; Coupe 2001; Fogel et al. 2002, Sajdak & Bartz 2004), and that females may exhibit more frequent arboreal activity than males (Coupe 2001). Additional observations reported here will help to clarify aspects of the arboreal behavior of *C. horridus.*

STUDY AREA AND METHODS

The study area was on and adjacent to the floodplain of the Angelina River in Nacogdoches Co., Texas. Specific study sites were the Stephen F. Austin Experimental Forest located 12 km SW of Nacogdoches (31° 30'N, 94° 47'W), and the Loco Bayou Hunt Club located 15 km WSW of Nacogdoches (31° 31'N, 94° 50'W). Habitat at both sites consisted of bottomland hardwood forest dominated by oaks (*Quercus* sp.), sweetgum (*Liquidamber styraciflua*) and hickories (*Carya* sp.); and adjacent upland forest dominated by loblolly and shortleaf pines (*Pinus taeda* and *P. echinata*), oaks (*Quercus* sp.) and a diverse array of other species. Portions of the bottomland habitats were subject to winter and spring flooding in most years.

Crotalus horridus were captured as encountered during the course of the study, transported to the laboratory, and implanted with SI-2T transmitters (Holohil Systems Ltd.). Transmitters were implanted subcutaneously following the general procedures of Reinert & Cundall (1982) and Weatherhead & Anderka (1984). Snakes were retained in the laboratory, with access to a heating pad, for approximately 7 d following surgery to facilitate healing. Transmitters were replaced at approximately 18 mo intervals.

Following release, snakes were relocated at irregular intervals, GPS locations recorded, and a series of habitat measurements and other data recorded as required for ongoing studies. In instances where individuals were located in arboreal situations, snake height, plant species, diameter at breast height (dbh) of supporting tree, presence of vines and other pertinent observations were noted.

A series of climbing trials using *C. horridus* were conducted on selected trees. Lengths of muscadine grape (*Vitis rotundifolia*) vines 3-6 cm in diameter were occasionally attached to tree trunks to simulate situations noted during climbing events. Observation of subsequent climbing behavior provided some indication of the arboreal abilities of *C. horridus.*

A series of feeding trials were also conducted using Brown-headed

Cowbirds (*Molothrus ater*). Cowbirds were captured in mist nets or box traps, placed in cages with individual *C. horridus* of various sizes, and the snakes' subsequent behavior recorded.

RESULTS

Thirty four *C. horridus* (60-140 cm SVL) were radio-tracked between 1993 and 2000 yielding more than 500 relocations. During this period 12 sub-adult snakes <90 cm SVL and with a mass <510 g were relocated a total of 218 times. Eight of these 12 snakes were located in arboreal situations a total of 35 times (Table 1). Each of the four snakes <90 cm SVL never found in an arboreal location were individuals represented by less than 10 relocation points. Snakes larger than 90 cm SVL, range 90-140 cm, were never observed in arboreal situations, with one exception. An adult male (136 cm SVL) was located in a shrub at heights ranging from 0.5 to 1.2 m on three occasions during a 15 day period. This individual had uncharacteristically occupied a hibernaculum in a bottomland hardwood site prone to flooding. In each arboreal observation the snake had been forced out of the hibernaculum and into the shrub by rising water. This observation is not included in the analyses that follow.

The 35 instances of arboreal behavior represent 16.1% (35 of 218) of total observations of snakes <90 cm SVL and 17.9% (35 of 196) of observations of those individuals located in arboreal situations at least once. Arboreal behavior was observed in all months from March to October, the general activity period of *C. horridus* in eastern Texas. Of the minimum of 21 separate climbing events, females were involved in 11, males in 10. Contingency table comparison of arboreal relocations vs. total relocations for females (18 of 147, 12.2%) and males (17 of 71, 23.9%) showed a slight, but significant bias favoring males ($\chi^2 = 3.88$. $P < 0.05$).

The heights at which *C. horridus* were located ranged from 0.8 – 14.5 m with a mean of 5.9 m based on the 23 distinct arboreal locations represented. Individual snakes were relocated in the same tree ($n = 9$), occasionally with minor movements ($n = 2$), during subsequent relocations ranging from three to 24 days. There is no way of knowing whether these individuals returned to the ground between observations. Instances where snakes were relocated in the same arboreal location on subsequent days were typically those located at greater heights, however the irregularity of the relocation schedule makes detailed comparisons difficult. In all cases where visual evaluation was possible, snakes were

Table 1. Snake measurements and arboreal behavior data for timber rattlesnakes (*Crotalus horridus*) in eastern Texas.

Snake	Date	SVL (cm)	Mass (g)	Tree Species	DBH (cm)	Snake Height (m)
Female #1	10 Aug. 93	65.4	173.5	*Carpinus caroliniana*	11	3.5
Female #1	5 & 10 May 94	75.4	282.6	*Quercus phellos*	40	7.0 & 9.0
Female #2	14 Sep. 95	87.5	498.8	*Carya* sp.	Small	2.0
Female #3	7 Aug. 96	80.1	450.4	*Quercus laurifolia*	42	14.5
Female #4	29 Sep. 95	78.2	430.3	vines	<2	2.3
Female #4	17 Sep. 96	89.7	503.0	*Quercus lyrata*	37	8.1
Female #5	31 Mar. 99	80.9	257.0	*Ilex decidua*	3	1.0
Female #5[1]	5-14 May 99	80.9	257.0	*Liquidambar styraciflua*	35	6.5
Female #5	18 & 21 May 99	80.9	257.0	*Quercus nigra*	14	6.5
Female #5	24 May & 17 Jun. 99	80.9	257.0	*Quercus muehlenbergii*	46	7.0 & 9.0
Female #5	23 & 29 June 99	80.9	257.0	Unidentified, dead	9.5	3.0
Male #1	2 & 5 Oct. 96	79.1	354.0	*Liquidambar styraciflua*	33	4.5
Male #1	10 Oct. 96	79.1	354.0	*Quercus phellos*	48	4.5
Male #1[2]	1 Mar.-8 Apr. 97	79.1	354.0	*Morus rubra*	23	4.5
Male #2	10 Jul. 97	59.8	127.0	vines	<2	0.8
Male #2	24 Jul. 97	59.8	127.0	*Quercus laurifolia*	13	11.3
Male #2	21 & 28 Aug. 97	59.8	127.0	*Quercus alba*	44	>8.0
Male #2	5 & 8 Sep. 97	59.8	127.0	*Carya* sp.	36	13.5
Male #2	23 Oct. 97	59.8	127.0	Unidentified	3	2.6
Male #2	5 May 98	85.5	508.5	Dead Limbs	?	2.5
Male #3	27 Mar. 97	84.5	488.0	*Quercus laurifolia*	25	2.5

[1] Four observations between 5 May and 14 May 1999.

[2] Five observations between 1 Mar. and 8 Apr. 1997.

coiled or variously extended along branches or in forks of trunks or major limbs. No instances were observed where snakes were coiled around supporting limbs or assumed specific postures to maintain stability in arboreal situations.

The arboreal situations occupied by *C. horridus* varied considerably. Of the minimum 21 distinct climbing events observed, six were situations where snakes were in vine tangles, dead tops of fallen trees, and small saplings or shrubs at heights of 2.6 m or less. In the remaining 15 instances, the snakes were located in substantial trees (9.5 – 48 cm DBH) at heights >2.5 m, often much greater. Vines, smaller diameter trees with low branches, loose bark and leaning trunks potentially facilitated the climbing in six of these instances. However, in the remaining nine instances the snakes were located in canopy or subcanopy trees (14 – 48 cm DBH) at heights of 4.5 – 14.5 m without obvious characteristics that would facilitate climbing. In the most extreme case, a *C. horridus* was located at a height of 14.5 m at the first major fork of a laurel oak (*Quercus phellos*). The trunk was vertical, with a clear bole, and no vines to facilitate climbing. Access to this site was limited to climbing the vertical trunk or via the canopies of adjacent trees.

Climbing trials with *C. horridus* <90 cm SVL demonstrated limited climbing ability compared to other species (*Elaphe* sp., *Masticophis flagellum*) that typically exhibit arboreal behavior. In cases where smaller branches were available *C. horridus* were able to maneuver slowly along horizontal or inclined branches, bridge between branches, and coil around branches to maintain a stable hold. However, it was not possible to elicit climbing of vertical, or nearly vertical, branches of any diameter, or boles of trees. Throughout these trials snakes gave the impression of awkwardness and hesitancy.

Eighteen laboratory trials were conducted in which birds (*Molothrus ater*) were presented to *C. horridus* of various sizes (range 75 – 104 cm SVL), and subsequent prey capture occurred. In all instances following the initial strike, the snakes maintained a hold on the bird until death of the bird. Time until apparent death of the cowbirds ranged from 54-364 sec with a mean of 188 sec. Feathers appeared to present a substantial impediment to fang penetration, and in several instances the snakes were observed to manipulate the cowbird between their jaws without releasing the bird, often for several min, until they were able to penetrate the feathers with a fang. Smaller snakes that did not immediately achieve an effective bite often had the anterior portion of their body moved around the cage by the struggles of the cowbirds. The overall behavior of the snakes striking birds was distinctly different from observations of these same snakes preying on a variety of mammalian species where prey was struck and immediately released.

DISCUSSION

Previously published accounts (Saenz et al. 1996; Coupe 2001; Fogel et al. 2002) and included references and communications, Sealy 2002; Sajdak & Bartz 2004; Bartz & Sajdak 2004) suggest that *C. horridus* consistently exhibits arboreal behavior and vindicates portions of Audubon's early observations. However, much remains to be learned about arboreal behavior in *C. horridus*, including prevalence, ontogenetic variation, geographic variation and motivation.

Size appears to limit arboreal behavior in *C. horridus*. Published accounts (Saenz et al. 1996; Coupe 2001; Fogel et al. 2002; Sajdak & Bartz 2004; Bartz & Sajdak 2994; this study) report only five individuals >90 cm SVL demonstrating arboreal behavior: two individuals (99.5 and 112.5 cm SVL) reported by Coupe (2001) without specific details, two individuals (100.5 and 98.0 cm SVL) reported by Bartz & Sajdak (2004) engaged in courtship approximately 1 m above the ground, and the adult male individual reported in this study at modest heights after being forced from its hibernaculum by rising water. The relationship between size and arboreal behavior has not been reported previously, with the exception of Saenz et al. (1996) preliminary report of this study, presumably due to the relatively small adult size of the more northern populations involved in most previous reports.

This study documents more extensive arboreal behavior by *C. horridus*, at least sub-adults, than previously reported (Coupe 2001; Fogel et al. 2002; Sajdak & Bartz 2004; Bartz & Sajdak 2004). Although Klauber (1972) characterized *C. horridus* as "among the more persistent climbers," arboreal behavior has been described as uncommon (Fogel et al. 2002), and characterized as frequent, rare, numerous instances, rarely observed (communications in Coupe 2001) without specific details. Only Coupe (2001) provides more specific data, stating that *C. horridus* were observed in arboreal situations during 13.2% of relocations; however, this figure is based on the subset of individuals observed in such situations at least once. In this study sub-adults were located in arboreal situations during 16.1% of relocations, and restricting the data to only those individuals observed in arboreal situations at least once (comparable to Coupe's 2001 data) raises this figure to 17.9%.

Obviously, these data are not directly comparable, primarily because *C. horridus* in the more northern populations rarely reach body lengths at which arboreal behavior becomes extremely rare in eastern Texas.

This study, including the preliminary observations reported by Saenz et al. (1996), is the first to report arboreal activity at substantial heights. Most previous reports are of individuals located at modest heights of 3 m or less, with a maximum of 5 m (Coupe 2001; Fogel et al. 2002; Sajdak & Bartz 2004). In eastern Texas the mean height of arboreal locations was 5.9 m with a maximum of 14.5 m, considerably higher than previously reported for this species. Sub-adult *C. horridus* were regularly located in the lower portions of tree canopies.

Arboreal behavior in *C. horridus* in eastern Texas appears to be more frequent and involve greater heights than is the case in more northern populations. It is important to realize, however, that this comparison is based on sub-adult individuals in eastern Texas, individuals comparable in size to most adults in more northern populations. These comparisons suggest that arboreal behavior is more prevalent in the more southern portions of the range of *C. horridus*. Additional data from a wider geographic range would be desirable.

Coupe (2001) suggested that arboreal behavior might be more prevalent among females. In eastern Texas, males were more frequently observed in arboreal situations based on percent of observations. Overall, currently available data do not demonstrate a consistent difference in arboreal behavior between females and males.

The motivation leading to arboreal behavior in *C. horridus* has elicited considerable speculation but little insight. Of the 23 individuals involved in a minimum of 41 separate climbs and observed on a total of 107 separate days reported in Coupe (2001), Fogel et al. (2002), Sealy (2002), Sajdak & Bartz (2004), Bartz & Sajdak (2004), and this study, two were associated with flood waters, three with ecdysis, one with basking by a gravid female, and four (2 pairs) with courtship. All of these observations were of individuals at heights <5 m, generally <3 m. Attaining a preferred thermal regime (basking) could conceivably be associated with several of the above observations and unrecognized in others. However, in Texas obvious basking behavior is rare. Individuals are generally exposed on the forest floor but do not seek open areas, track sun flecks, or show other behaviors that could be associated with basking. Even gravid females, which typically seek heavy cover (hollow logs, debris piles), do not need to bask given the relatively high average temperatures in the region. Consequently, basking and other activities noted above can only account for a minority of the observations, and do not appear to be involved in the observations at more extreme heights. These considerations may not even represent the primary motivation that led to the initial climbing activity in all cases.

Avoidance of terrestrial predators is potentially a factor leading to arboreal behavior. If restricted to periods when active foraging is not occurring (ecdysis, post-feeding periods after mobility is regained) benefits might result. However, data or observations that support this hypothesis are not available.

Arboreal foraging is a possibility mentioned by Klauber (1972), Saenz et al. (1996), Fogel et al. (2002), and Coupe (2001). Arboreal foraging was verified in one instance (Sajdak & Bartz 2004) when a was observed capturing a Yellow-bellied Sapsucker (*Sphyrapicus varius*) at a height of 4.5-6 m. Verification of arboreal foraging behavior is difficult because definitive foraging postures in arboreal situations, analogous to those described in terrestrial situations (Reinert et al. 1984), have not been recognized. *Crotalus horridus* preys primarily on endotherms (Clark 2001). Consequently, potential prey available in arboreal situations in Texas are restricted to numerous species of birds, southern flying squirrels (*Glaucomys volans*), squirrels (*Sciurus* sp.) and a limited variety of other small mammals. In a recent compilation of the prey of *C. horridus*, Clark (2001) reported that approximately 7% of recorded prey items were birds, although a substantial number of those identified to species were primarily terrestrial. Squirrels of the genus *Sciurus*, the primary prey of adult *C. horridus* in eastern Texas are often abundant in arboreal situations. However *Sciurus* sp., and in many cases even *G. volans*, are too large for *C. horridus*, of the sizes that typically climb, to handle.

Birds would seem to be the most likely prey of *C. horridus* in arboreal situations. Climbing and predation on birds has been observed in other pitvipers. The shedao pitviper (*Gloydius shedaoensis*) in China, a relatively thick-bodied pitviper where adults average 60-70 cm SVL, actively climbs trees and shrubs and ambushes birds primarily during periods of avian migration (Shine et al. 2002). Striking and holding avian prey, presumably a secondarily acquired trait in Crotalids that prey regularly on mammals (Martins et al. 2002; Stiles et al. 2002), may increase the efficiency of predation on birds. Striking and holding onto avian prey was the strategy used in the report of Sajdak & Bartz (2004), even during a minimum vertical fall of 3 m to a lower branch. Mammalian prey that is potentially more dangerous to *C. horridus* is typically released immediately after striking (Chiszar et al. 1982; Stiles et al. 2002). Strike and release would present significant difficulties in trailing prey that could fly, even for short distances, and would presumably be extremely difficult from arboreal situations (Martins et al. 2002). Observations of prey taxa, that present little potential danger or are potentially difficult to trail or handle, that various Crotalids strike and hold include scorpions, fishes, frogs, lizards and birds (Parker & Stotz 1977; Rubio 1998; Hayes & Duvall 1991; Reiserer 2002; Stiles et al. 2002).

The limited climbing abilities of *C. horridus* may limit the possibilities of arboreal foraging to smaller snakes. The apparent lack of behaviors such as coiling around limbs for support, or specialized support postures used by other heavy bodied arboreal species would appear to limit the ability of *C. horridus* to capture and handle prey items in arboreal situations. The report by Sajdak & Bartz (2004) of the *C. horridus* falling to a lower branch during prey capture supports this view. Despite these limitations, foraging remains the most likely general explanation for arboreal behavior in *C. horridus*.

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NESTING HABITAT OF EASTERN WILD TURKEYS (*MELEAGRIS GALLOPAVO SYLVESTRIS*) IN EAST TEXAS

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Abstract.—Eastern wild turkeys (*Meleagris gallopavo sylvestris)* captured in Iowa and Georgia were relocated to the Pineywoods of east Texas where they were radio-marked and released. During the 1995 and 1996 nesting seasons, nest sites of radio-marked hens were located and characteristics of the habitat surrounding the sites and of randomly selected sites in the same vegetation type were evaluated using paired *t*-tests. Of 24 nest located, 6 were successful. Most nests were in mature pine-hardwood stands or pine regeneration areas. Nest sites had higher densities of living and dead grasses and higher screening cover values than did random sites ($P < 0.05$). Other habitat characteristics did not differ between nest and random sites ($P > 0.05$). These results suggest that herbaceous ground cover is the most important habitat variable which hens use when selecting nest sites. Habitat characteristics surrounding nests located in this study were similar to those documented in other studies in the southeast. Although nesting habitat probably is adequate in east Texas, land managers could increase such habitat by mowing utility rights-of-way on a two to three-year schedule, implementing a three to five-year prescribed burning regime, thinning pine stands at or before canopy closure, retaining slash after logging operation, and delaying site preparation in regeneration areas until after the nesting season.

In Texas, the eastern wild turkey (*Meleagris gallopavo sylvestris*) originally ranged over approximately 12,145,000 hectares in 40 counties in the Pineywoods Ecological Region (Newman 1945). The birds occupied river bottom and upland forest communities. During the 1800's, Texas settlers thought eastern wild turkey populations to be inexhaustible (Carpenter 1959). However, commercial hunting and extensive land clearing led to declining turkey numbers throughout the early 1900's (Carpenter 1959). In 1941, the Texas Legislature closed the turkey season throughout the Pineywoods, but the action came much too late; by 1942, less than 100 native eastern wild turkeys remained in Texas (Newman 1945).

Records indicate that wild turkey restoration efforts by the Texas Game, Fish and Oyster Commission began in east Texas as early as 1924 (Newman 1945; Carpenter 1959). Many unsuccessful restocking attempts were made during the next 40 to 50 years; most failed attempts used pen-reared eastern wild turkeys or the Rio Grande subspecies (*M. gallopavo intermedia*). However, between 1979 and 1981, wild-trapped eastern wild turkeys were released on two east Texas sites, and populations flourished (Swank et al. 1985). In 1987, the Texas Parks and Wildlife Department, in cooperation with the National Wild Turkey Federation, initiated a large-scale eastern wild turkey restoration program in east Texas. The program used wild-trapped eastern turkeys acquired from southeastern and midwestern states. Some restockings were successful, but others failed and populations remained low in many areas (J. D. Burk, per. comm.).

Wild turkey populations are sustained by annual brood productivity (Seiss et al. 1990). Thus, nesting habitat is critical to the well-being of the species (Badyaev 1995). In order to increase wild turkey productivity in east Texas, suitable nesting habitat needs to be identified. The objectives of this study were to describe vegetative characteristics surrounding nest sites of wild turkey hens and to compare these characteristics to vegetative characteristics surrounding random sites.

METHODS

Four study areas in Tyler County, Texas were stocked with wild-trapped eastern wild turkeys relocated from Iowa and Georgia during January and February of 1994. Twelve hens and three gobblers were released at each site; equal numbers of hens and gobblers were from Iowa and Georgia. Prior to release the turkeys were aged, banded and fitted with back-pack style radio transmitters. An attempt was made to radio-locate the birds daily for the first two weeks after release. If mortality occurred during that period, the bird was replaced. Thereafter, the birds were radio-located at least once a week, and up to three times a week. During February 1995, eight wild turkey hens were captured on a study area in Trinity County; the birds were aged, banded, fitted with transmitters and released at the point of capture. In January of 1996, an additional 15 wild-trapped hens from Iowa were fitted with transmitters and released on that study area.

Beginning on 1 April of 1995 and 1996 hens were radio-located three to five times per week. When a hen exhibited very localized daily movements, it was assumed she had initiated a nest. Once a hen was radio-located three times in the same place, it was assumed incubation had begun, and she was radio-located daily. After approximately 10 days of incubation, the nest location was estimated using triangulation, azimuths, and estimated observer-to-nest distances. After the hen had left the nest area for at least one day, an attempt was made to locate and determine the fate of the nest. Nests were classified as successful (≥ one egg hatched) or unsuccessful (depredated or abandoned).

Macro and micro-habitat characteristics were evaluated at each nest location. The macro-habitat variables were forest type and tree size class. Forest type of the stand surrounding each nest was classified as either pine, pine-hardwood, riparian or opening; openings included food plots, rights-of-way, pastures and seedling (≤ 1.4 m tall) pine plantations. Tree size classes (trees > 1.4 m tall) were based on diameter at breast height (DBH) of dominant trees in the area surrounding the nest site. Size classes used were sapling (< 12.7 cm DBH), pole (12.7 to 27.9 cm DBH) and sawtimber (≥ 27.9 cm DBH) (Stoddard & Stoddard 1987).

Chi-square tests were used to determine if nesting hens selected macro-habitats according to availability. Habitat composition data from a study by George (1997) were used with Chi-square tests for Tyler County nests. In that study, macro-habitats were classified as pure pine forests, pine-hardwood forests, riparian forests or openings. Habitat composition data for the Trinity County study area were gathered from the Temple-Inland Forest Products Corporation five-year plan for the area; macro-habitats were categorized the same as the George (1997) study.

Micro-habitat data were collected in the area immediately surrounding the nest site. Micro-habitat characteristics measured included basal area of pine, basal area of hardwood, total basal area, distance to nearest man-made edge, distance to nearest natural edge, percent canopy closures, relative screening cover of the understory and relative densities of the ground cover.

Basal areas were measured from the center of the nest using a 10-factor prism. Distances to nearest man-made and natural edges were measured using a 23-m logger's tape. Canopy closures of the understory, midstory and overstory were evaluated using a modified point-quadrat technique (Smeins & Slack 1982). Understory was vegetation < 2 m tall, midstory 2 to 15 m tall, and overstory vegetation > 15 m tall. With the nest as the plot center, a 10-m transect was established in each cardinal direction. Along each transect, five subpoints were spaced at 2-m intervals; the first subpoint on each transect was 2 m from the nest site. Canopy closure data were gathered at each subpoint using a sighting tube (Whiting & Fleet 1987; Parsons 1994). At each subpoint, an observer looked straight up or down through the sighting tube, and for each height class, if vegetation obstructed the crosshairs, "yes" was recorded. From this procedure, a percent closure score could be calculated for each canopy layer.

Understory vegetation cover was evaluated in five strata between ground level and 1.7 m above ground level. Each of the lower four strata were 30 cm wide; the top stratum was 50 cm wide. Screening cover data were gathered using a vegetation profile board (VPB). The VPB was 1.7 m tall, 8.9 cm wide and divided into five alternating red and white colored sections which corresponded to the five strata evaluated. The board was placed at the nest center and the percent of each section obscured was estimated from a distance of 15 m and a height of approximately 46 cm (Nudds 1977). Scores were based on a scale of one to five and reflected the percentage of the board which was obscured by vegetation. Scores of one, two, three, four and five, indicated 0 to 20%, 21 to 40%, 41 to 60%, 61 to 80% and 81 to 100% obscurity, respectively. Screening cover scores were estimated from each cardinal direction by stratum. These values were then averaged to provide percent screening cover for each stratum.

Relative density of ground cover (i.e., living or dead vegetation) was evaluated using a point quadrat technique. A 10-pin frame was used to sample ground cover within 60 cm of the ground (Parsons 1994). The pin frame measured 80 cm high and 110 cm long; pins were centered at 10-cm intervals along the frame. Data were gathered at five subpoints around each nest site. For the first subpoint, the pin frame was centered on the actual nest bowl. The remaining four subpoints were 15 m from the nest in the cardinal directions. At each subpoint, the pins were lowered from approximately 60 cm and each pin-to-plant hit was recorded by plant category (i.e., living woody, herbaceous, grass or dead grass). These data were used to derive an index of relative density for each plant category. This index was simply the number of hits by category per 10 pins (i.e., an index of 31 for living grasses would indicate that the 10 pins made 31 contacts with living grasses). The last hit recorded for each pin was either litter or soil. As each pin could have only one contact with either litter or bare soil, numbers of hits were converted to percentages. Average height of ground cover, as bracketed by the pin frame, also was measured at each subpoint.

Immediately after micro-habitat measurements of a nest location were completed, micro-habitat data were collected from a random location in the same macro-habitat type (forest type and stand class). Standing at the nest, the observer glanced at the second hand of his wristwatch and used the direction it was pointing as a random direction. Using a compass, the observer then paced a distance which had been previously taken from a random numbers table; minimum and maximum acceptable distances were 100 m and 250 m, respectively. Data gathered at random locations were the same as those gathered at nest locations. Differences in micro-habitat variables between nest sites and random sites were evaluated using paired *t*-tests; all tests were performed at a 0.05 alpha level.

RESULTS

At the beginning of the 1995 and 1996 nesting seasons, there were 37 and 44 hens, respectively, with active transmitters. Although eight hens died or were lost between the 1995 and 1996 nesting seasons, 15 additional Iowa hens were released on the Trinity County site, thus increasing the sample size by seven. During the two nesting seasons, 24 nests were located, 11 in 1995 and 13 in 1996; six nests were successful and 18 were unsuccessful. Twelve nests were in Trinity County, and 12 nests were in Tyler County; the six successful nests were in Tyler County.

The majority of nests were in pine-hardwood habitat types (11) and openings (8) (Eichler 1999:20). In both counties, there were differences between habitat availability and habitats selected for nesting (Table 1). In Tyler County, openings made up only 21.0% of the study area, yet six hens (50.0%) selected this habitat type in which to nest. Conversely, only one nest was in a pine-hardwood stand and this habitat type made up 27.2% of the study area (χ^2 = 23.00, 3 df, *P* = 0.001) (Table 1). In Trinity County, ten of 12 (83.3%) nests were in pine-hardwood stands which comprised 55.0% of the study area. Although riparian forests comprised 36.0% of the area, no hens nested in that habitat (χ^2 = 52.23, 3 *df*, *P* = 0.001).

Thirteen of the 24 nests were in sawtimber stands; 11 were in pine-hardwood forests and two were in riparian forests. Eight nests were in openings; of these, four were in pine seedling stands ≤ two years old, two in an abandoned field, one in a grazed field, and one in the thick vegetation (i.e., rough) bordering a food plot. The remaining three nests were in sapling and pine pole stands. Four successful nests were in openings (all were pine seedling stands ≤ two years old), one in a pine sapling stand, and one in a pine pole stand.

Table 1. Habitat availability and use of habitat types and stand classes by nesting eastern wild turkey hens in east Texas, spring 1995 and 1996. Habitat composition differed from utilization rates at Tyler County sites (X^2 = 23.00, 3 *df*, $P<0.001$) and Boggy Slough sites (X^2 = 52.23, 3 *df*, $P<0.001$).

	Tyler County			Boggy Slough				
	Habitat composition	Nests		Habitat composition	Nests		All nests	
Habitat	(%)	(No.)	(%)	(%)	(No.)	(%)	(No.)	(%)
Habitat type								
Pure pine	30.7	3	25.0	4.0	0	00.0	3	12.6
Pine-hardwood	27.2	1	8.3	55.0	10	83.3	11	45.8
Riparian	21.1	2	16.7	36.0	0	00.0	2	8.3
Opening	21.0	6	50.0	5.0	2	16.7	8	33.3
Total	100.0	12	100.0	100.0	12	100.0	24	100.0
Stand class								
Opening		6	50.0		2	16.7	8	33.3
Sapling		2	16.7		0	00.0	2	8.3
Pole		1	8.3		0	00.0	1	4.2
Sawtimber		3	25.0		10	83.3	13	54.2
Total		12	100.0		12	100.0	24	100.0

Some micro-habitat variables differed between nest sites and random sites (Table 2). In all strata, screening cover values at nest sites were higher than those at random sites; the differences were significant in the 0.31 to 0.60 m and the 1.21 to 1.70 m strata and approached significance in the 0.00 to 0.30 m stratum (Table 2) . The largest difference was in the 0.31 to 0.60 m stratum where screening cover averaged about 14% higher at nest than at random sites. Ground cover densities were greater at nest than at random sites for all except the herbaceous category. Ground cover densities for both living grass and dead grass were significantly higher at nest sites than at random locations (Table 2). Although not statistically significant, canopy closures in the midstory were more open at nest sites than random locations (Table 2).

DISCUSSION

In this study, hens selected pine habitat types and openings in which to nests. Previous studies in the Southeast have shown similar results (Campo et al. 1989; Seiss et al. 1990; Sisson et al. 1990; Still & Baumann 1990). In a previous east Texas study, 89% of the nests were in upland pine forest types; however, as opposed to this study, those nests were equally distributed among size classes of timber (Campo et al. 1989). In South Carolina, Still & Baumann (1990) found 21 of 37 nests in pine habitats and in Georgia, Sisson et al. (1990) found 83% of all nests in pine stands. However, in Mississippi, mature pine stands

Table 2. Results of paired *t*-tests (24 *df*) comparing micro-habitat characteristics of eastern wild turkey nest sites to random sites (n = 24) in east Texas, 1995-1996.

Habitat component	Nest sites	Random sites	*t*	*P*
Distance from edge (m)				
Natural	39.3	42.7	0.298	0.769
Manmade	40.0	35.7	0.449	0.658
Basal area (m^2/ha) [a]				
Pine	11.2	12.4	-0.834	0.413
Hardwood	5.7	5.20	-0.290	0.775
Total	17.0	17.6	-1.000	0.327
Canopy coverage (%) [a]				
Understory (<2 m)	57.8	56.7	-0.249	0.805
Midstory (2-15 m)	53.9	60.8	-2.029	0.054
Overstory (>15 m)	42.2	44.7	-1.334	0.195
Screening cover (%)				
0.00 - 0.30 m	93.3	86.7	2.205	0.055
0.31 - 0.60 m	79.4	65.4	2.893	0.008
0.61 - 0.90 m	64.4	53.1	1.450	0.161
0.91 - 1.20 m	58.1	49.6	1.228	0.232
1.21 - 1.70 m	46.9	33.8	2.328	0.029
Ground cover density (hits / 10 pins)				
Living grass	31.7	25.3	2.559	0.018
Dead grass	10.4	3.1	2.119	0.045
Herbaceous	6.5	6.7	-0.073	0.942
Woody species	13.2	10.9	1.239	0.228
Litter (%)	88.4	89.0	-0.187	0.854
Height of ground cover (cm)	25.8	23.5	0.965	0.354

[a] Only tested in sapling, pole and sawtimber stands.

contained the most nests (18 of 38) but were used according to availability (Seiss et al. 1990). In that study, other habitats in which hens nested included bottomland hardwoods and pine and hardwood regeneration areas.

Use of early successional habitats for nesting is also similar to findings of other studies (Everett et al. 1981; Campo et al. 1989; Seiss et al. 1990; Still & Baumann 1990). Seiss et al. (1990) found 36.8% of all nests in regeneration areas whereas that type made up only 12.5% of available habitat. In South Carolina, Still & Baumann (1990) found 10 of 37 (27%) nests in seed-tree cuts or clearcuts ≤ 10 years old, and in a previous east Texas study, 26% of the hens nested in pine regeneration stands one to seven years old (Campo et al. 1989); in this study 25.0% of hens nested in regeneration areas. Everett et al. (1981) found that rights-of-way with roughs one to three years old were preferred nesting habitat in Alabama.

Prescribed burning may be an important factor for nest site selection. In Trinity County, 10 of the 12 nests were in pine uplands which were burned on a three to five-year regime. These results are similar to those of Sisson et al. (1990) who found that most nests (74%) were in upland pine stands on a one to three-year burn rotation; in that study, such stands comprised only 7.2% of the area. Conversely, in Alabama, Exum et al. (1987) found 89% of nesting hens used areas left unburned for three or more years.

In 1996, three of seven nests in Trinity County were in pine sawtimber stands which had been thinned < two months prior to nesting season. All three nests were concealed by logging slash. Previous studies have shown that hens prefer nesting in thinned stands (Hillestad 1973; Lutz & Crawford 1987; Campo et al. 1989) and use logging slash as concealment (Martin 1984; Lutz & Crawford 1987; Swanson 1993). Hillestad (1973) found that four of seven hens selected recently cut-over loblolly pine, shortleaf pine, or sweetgum stands in which to nest. In Oregon, Lutz & Crawford (1987) found that nesting hens used thinned conifer stands more frequently than expected ($P < 0.05$) and that nests were commonly adjacent to slash.

In this study, nests sites had abundant screening cover in the 0.00 - 0.30 and 0.31 - 0.60 m strata with values ranging from 80-95%. Nests sites in pole and sawtimber stands had lower basal area and canopy closure values than did random sites (Eichler 1999), and higher densities of living grasses and woody seedlings. These results parallel those of other studies which have shown that nest sites normally have lower densities of overstory trees, basal areas and canopy closures, and higher screening concealment than do random locations (Lazarus & Porter 1985; Holbrook et al. 1987; Lutz & Crawford 1987; Campo et al. 1989, Still & Baumann 1990, Swanson 1993; Lopez 1996). In the Post Oak Savannah Region of east Texas, nest sites occurred in areas with relatively high coverage of forbs in the understory and ground layers (Lopez 1996). Still & Baumann (1990) found that nesting hens preferred low to moderately stocked stands, suggesting that ground cover was important. Holbrook et al. (1987) found that cover below the 2-m level was more dense around nests than at random locations.

Characteristics of habitats used by nesting hens in this study were very similar to those in other studies in the Southeast. These results suggest that nesting habitat is adequate in east Texas (Eichler 1999).

However, there are several practices which land managers could use to increase nest success. This study indicated that herbaceous ground cover is the most important habitat variable hens use when selecting nest locations. In forested stands, a three to five-year burning regime would seem to be appropriate to stimulate and maintain herbaceous densities for nesting throughout the Pineywoods of east Texas. Additionally, thinning pole and sawtimber stands would allow for this same type of ground cover. After logging operations, slash and tree tops should be left as is to provide cover at least until after the nesting season. Likewise, in newly created regeneration areas, site preparation practices should be delayed until after the nesting season when possible. Lastly, utility rights-of-way should be mowed on a two to three-year schedule; a mosaic of two to three-year roughs would allow for nesting habitat and discourage the growth of brush thickets.

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THE RED-COCKADED WOODPECKER: INTERACTIONS WITH FIRE, SNAGS, FUNGI, RAT SNAKES AND PILEATED WOODPECKERS

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Abstract.—Red-cockaded woodpecker (*Picoides borealis*) adaptation to fire-maintained southern pine ecosystems has involved several important interactions: (1) the reduction of hardwood frequency in the pine ecosystem because of frequent fires, (2) the softening of pine heartwood by red heart fungus (*Phellinus pini*) that hastens cavity excavation by the species, (3) the woodpecker's use of the pine's resin system to create a barrier against rat snakes (*Elaphe* sp.), and (4) the woodpecker as a keystone cavity excavator for secondary-cavity users. Historically, frequent, low-intensity ground fires in southern pine uplands reduced the availability of dead trees (snags) that are typically used by other woodpecker species for cavity excavation. Behavioral adaptation has permitted red-cockaded woodpeckers to use living pines for their cavity trees and thus exploit the frequently burned pine uplands. Further, it is proposed that recent observations of pileated woodpecker (*Dryocopus pileatus*) destruction of red-cockaded woodpecker cavities may be related to the exclusion of fire, which has increased the number of snags and pileated woodpeckers. Red-cockaded woodpeckers mostly depend on red heart fungus to soften the heartwood of their cavity trees, allowing cavity excavation to proceed more quickly. Red-cockaded woodpeckers use the cavity tree's resin system to create a barrier that serves as a deterrent against rat snake predation by excavating small wounds, termed resin wells, above and below cavity entrances. It is suggested that red-cockaded woodpeckers are a keystone species in fire-maintained southern pine ecosystems because, historically, they were the only species that regularly could excavate cavities in living pines within these ecosystems. Many of the more than 30 vertebrate and invertebrate species known to use red-cockaded woodpecker cavities are highly dependent on this woodpecker in fire-maintained upland pine forests.

The red-cockaded woodpecker (*Picoides borealis*) evolved in a landscape where frequent, low-intensity fires burned within upland southern pine ecosystems. The fires reduced the numbers of hardwoods, and it is suggested that they also reduced the numbers of dead trees (snags) relative to their abundances in hardwood stands along riparian areas and bottomlands (Conner et al. 2001a). Hardwood snags, which serve as typical cavity trees for many woodpecker species in this scenario, were probably scarce. It was in this landscape that the red-cockaded woodpecker adapted to excavating cavities in live pine trees.

The extended length of time required to excavate cavities in live pines and the subsequent rarity of completed cavities in this ecosystem appear to be closely linked to the evolution of cooperative breeding in the red-cockaded woodpecker (Walters et al. 1988; 1992; Conner & Rudolph 1995). Cavities for nesting and roosting in living pines require a long time to excavate (Conner & Rudolph 1995; Harding & Walters 2002) and are so rare across the pine forest landscape that it is to the advantage of young woodpeckers, particularly young males, to forego dispersal and defer breeding until a breeding slot opens up in their natal cluster of cavity trees or a nearby cavity-tree cluster (Walters et al. 1992). These young woodpeckers from previous nesting efforts remain with the breeding pair and assist in subsequent nesting efforts by incubating eggs, feeding and brooding young, excavating cavities, and helping to defend the group's territory (Ligon 1970; Walters et al. 1988; Conner et al. 2001a).

In this paper a scenario is suggested by which historically frequent, low-intensity ground fires in southern pine uplands reduced the availability of dead trees (snags) that are typically used by woodpeckers for cavity excavation. Standing dead trees were more abundant in the more mesic hardwood sites where other species of woodpeckers are abundant. Behavioral adaptations permitted red-cockaded woodpeckers to excavate cavities into living pines for nesting and roosting. Thus, red-cockaded woodpeckers exploited the frequently burned pine uplands (Conner et al. 2001a), where the rarity of more typical cavity-excavation sites in dead branches and dead trees historically excluded or decreased the abundance of other woodpecker species in the southeastern United States because they typically do not make cavities in live pines (Conner et al. 1975; Kilham 1983). Discussion is also presented on how the woodpecker's adaptation to pine ecosystems has benefited other species by creating cavities in a relatively cavity-barren landscape.

THE INTERACTION OF FIRE WITH UPLAND PINE LANDSCAPES

Fossil pollen records indicate that fire-maintained pine ecosystems began to spread from peninsular Florida approximately 12,000 years ago and arrived at the western extreme of their distribution in Texas about 4,000 years ago (Webb 1987). This expansion was permitted by the retreat of the Laurentide ice sheet of the Wisconsin glaciation to the north (Conner et al. 2001a). Bartram (1791) described the original longleaf pine (*Pinus palustris*) forests as nearly unbroken expanses of widely spaced pines within a sea of grass. Fire, which burned in both the winter and growing season, was an integral part of the spread of pine ecosystems (Bonnicksen 2000; Conner et al. 2001a). Historically, frequent fires were ignited primarily during dry periods by lightning, Native Americans, and early settlers (Catesby 1731; Michaux 1802). The frequent fires burned day and night and meandered across the landscape until they encountered sites too isolated or too wet to burn (Frost 1993; Glitzenstein et al. 1995). The fires killed invading hardwoods in the upland pine ecosystem and maintained the herbaceous ground cover that consisted primarily of grasses and forbs (Jackson et al. 1986; Glitzenstein et al. 1995). Throughout the South, fallen pine needles and dried grasses served as fuel for the ground fires, which burned every one to three-plus years (Landers 1991; Glitzenstein et al. 1995; Bonnicksen 2000). Michaux's (1802) observations indicate that longleaf pine forests which occupied seven-tenths of the landscape in the Carolinas were burned annually.

Because hardwoods were rare in well-burned pine uplands (Chapman 1909; Platt et al. 1988; Frost 1993), live pines and pine snags were the primary sources of potential nest sites for woodpeckers. Although low-intensity ground fires may burn existing snags created by lightning and bark beetle (*Dendroctonus* sp., *Ips* sp.) infestation, they typically do not generate sufficient heat to kill pines, which would create new snags (Conner 1981; Conner et al. 2001a). Therefore, it is suggested that even pine snags may have been scarce in southern pine ecosystems.

INTERACTION OF RED-COCKADED WOODPECKERS WITH FUNGI

The use of living pines as sites to excavate cavities for nesting and roosting resulted in an increase in the length of time required for the woodpeckers to make a cavity. Most woodpecker species in eastern North America can excavate a new cavity in a dead, decayed snag in two to four weeks (Conner et al. 1975; 1976; Kilham 1983). Pileated woodpeckers (*Dryocopus pileatus*) can excavate a cavity in 23 days in the eastern United States, but excavation time can take three to six weeks in the Pacific Northwest (Bull & Jackson 1995). Downy woodpeckers (*Picoides pubescens*) can excavate a complete cavity in two weeks, whereas hairy woodpeckers (*Picoides villosus*) can take up to four weeks (Kilham 1983). Red-bellied woodpeckers (*Melanerpes carolinus*) typically can excavate a completed cavity within two weeks (Shackelford et al. 2000) and red-headed woodpeckers (*Melanerpes erythrocephalus*) within three weeks (Jackson 1976). Cavity excavation by northern flickers (*Colaptes auratus*) can take up to four weeks (Burns 1900). Lawrence (1967) observed that average cavity excavation time for northern flickers was 12.1 days, hairy woodpeckers 19.7 days, downy woodpeckers 16.0 days, and yellow-bellied sapsuckers (*Sphyrapicus varius*) 19.7 days.

Because red-cockaded woodpeckers use living pines for cavity trees, where the heartwood is often not decayed (Conner & Locke 1982), cavity excavation may require numerous years (Conner & Rudolph 1995). Unlike snags, which often have decayed sapwood and heartwood, the sapwood of live pines is not decayed (Conner & Locke 1982), and red-cockaded woodpeckers have to excavate through 8 to 16 cm of solid wood (Conner et al. 1994). Increasing sapwood thickness and the presence of flowing pine resin that seeps from the wound caused by cavity excavation further complicates the process and slows the rate of excavation (Conner et al. 1994; Conner & Rudolph 1995; Conner et al. 2001a). If resin flow is abundant, the woodpeckers typically must wait for the resin to crystallize before recommencing excavation, again, increasing the time required for cavity excavation (Conner & Rudolph 1995). Cavity excavation rates in red-cockaded woodpeckers may be influenced by the availability of suitable cavities (Harding & Walters 2002). As the need for cavities increases within a group of woodpeckers, the birds may accelerate their excavation activities (Conner et al. 2002).

Although red-cockaded woodpeckers can excavate a completed cavity into a pine with undecayed heartwood and sapwood (Conner & Locke 1982), the presence of red heart fungal (*Phellinus pini*) decay in the heartwood has an influence on the time required to excavate a complete cavity (Conner & Rudolph 1995). Red-cockaded woodpeckers are able to detect the presence of the fungus within the boles of the pines and actively select pines with red heart fungal decay for cavity trees (Conner & Locke 1982). Red heart fungus enters the heartwood of pines via broken branch stubs (Conner & Locke 1982; Conner et al. 2004). After gaining access to the heartwood of a pine, at least 15 to 20 years of growth and decay within the heartwood are required before the fungus produces a sporophore (conk) on the bole of the pine (Conner et al. 2004). This same 15- to 20-year time period is required for the fungus to decay a minimally sufficient diameter of heartwood (12 cm; Conner et al. 2004) for a woodpecker cavity. Although the age of the pine appears to be the primary factor associated with increasing frequency of heartwood decay (Conner et al. 1994), tree spacing and growth rate also have an influence (Conner et al. 2004). Older pines tend to have higher frequencies of heartwood decay and pines growing slowly in diameter prune lower branches more slowly and appear to have higher frequency of heartwood decay (Conner et al. 2004). Increased time during the natural limb pruning process allows more time for spores to infect wood tissue.

As red heart fungus decays the heartwood it softens the wood, and decayed heartwood is more easily excavated than sound heartwood. The presence of decayed heartwood can decrease the time required for cavity excavation by 1.3 years (Conner et al. 1994). Even with heartwood decay present in many cavity trees, an average of 1.8 years in loblolly (*Pinus taeda*) (*n* = 9 excavations), 2.4 years in shortleaf pines (*P. echinata*) (*n* = 12 excavations), and 6.3 years in longleaf pines (*n* = 12 excavations) is required to fully excavate a cavity (Conner & Rudolph 1995). Many red-cockaded woodpecker cavity trees are lost annually to bark beetles, lightning, wind action, and enlargement by pileated woodpeckers (Conner et al. 1991). Thus, the availability of pines infected with red heart fungus may determine whether red-cockaded woodpeckers have a sufficient number of useable cavity trees available for nesting and roosting in a given year.

INTERACTION OF RED-COCKADED WOODPECKERS WITH RESIN AND RAT SNAKES

Adaptation to contending with resin that flows from living pines when cavities are excavated has affected the interaction between red-cockaded woodpeckers and rat snakes (*Elaphe* sp.) and enhanced the survival of the woodpecker. Southern pines produce and maintain pine resin (gum) within an elaborate system of canals and ducts that extends from the pine's needles down into its roots. Resin is a mixture of primarily light resin oils (monoterpenes), which serve as solvents, and the heavier resin acids (diterpenes), which give the resin its viscous and sticky nature (Hodges et al. 1977).

The resin system in pines has evolved as their primary defense against bark beetles (Hodges et al. 1979). When bark beetles attack, the pine flushes the wound with resin and if sufficient resin is present, the attacking beetles are "pitched out." A similar response occurs when red-cockaded woodpeckers initiate cavity excavation. If resin flow is very high, it will temporarily interfere with cavity excavation as noted previously.

Red-cockaded woodpeckers nesting and roosting in living pines are extremely vulnerable to predation by rat snakes (Neal et al. 1993). Predictable, long-term use of individual cavities allows the local snake population to learn the location of cavities (Neal et al. 1993), and living pines with intact bark are easily climbed by rat snakes (Rudolph et al. 1990b). However, red-cockaded woodpeckers derive substantial protection from rat snakes by taking advantage of resin produced by pines to establish a resin barrier that prevents access to cavities by rat snakes. As cavities approach completion, red-cockaded woodpeckers excavate a series of small (1-2 cm) wounds into the cambium on the pine's bole around and above and below their cavity entrance. These wounds, termed resin wells, are pecked daily by the woodpeckers and the repeated pecking causes continuous wounding of the xylem-cambial boundary, keeping a stream of clear, fresh pine resin flowing from the wells and down the pine's bole. Multiple resin wells on a healthy cavity tree create a substantial barrier of sticky fresh resin that serves as a deterrent to climbing rat snakes (Ligon 1970; Jackson 1974; Rudolph et al. 1990b). However, repeated wounding of cavity trees over several years can decrease the ability of the pines to produce resin (Conner et al. 2001b) and pines with inadequate resin flow are abandoned by the woodpeckers (Conner & Rudolph 1995). Red-cockaded woodpeckers must continue to excavate new cavities to replace cavities with inadequate resin barriers and cavity trees lost to mortality factors or cavity enlargement by other woodpeckers.

Red-cockaded woodpeckers can detect how much resin a pine can produce (Conner et al. 1998). The socially dominant breeding male red-cockaded woodpecker selects the cavity tree that produces the most resin for his roost cavity. It is the breeding male's roost tree that usually becomes the breeding pair's nest tree. By selecting the cavity tree with the highest resin yield, the nesting effort of the breeding pair seems to receive the highest protection possible from rat snake predation (Conner et al. 1998).

Red-cockaded Woodpeckers as a Keystone Cavity Excavator

In the historic fire-maintained upland pine ecosystems of the South where pines existed nearly as a tree monoculture (Chapman 1909; Platt et al. 1988; Frost 1993), red-cockaded woodpeckers were the only woodpeckers able to excavate complete cavities in living pines regularly (Ligon 1970; Conner et al. 2001a). Reports of other North American species of woodpecker excavating cavities in live portions of living pines in the eastern United States are extremely rare or nonexistent (Bent 1939; Reller 1972; Conner et al. 1975; Jackson 1976; Kilham 1983). Red-cockaded woodpeckers historically were and continue to be a keystone species because they are the primary woodpecker species to provide cavities for more than 30 other wildlife species within fire-maintained pine ecosystems of the South (Table 1).

If dead trees were rare because they were consumed by the frequent ground fires, other woodpecker species and cavities created by them were likely also rare. Data on woodpecker species use of well-burned open pine habitats versus mixed pine-hardwood habitats support the argument that other woodpecker species were less abundant in the historic fire-maintained pine forests of the South than in habitats where hardwoods were present (Shackelford & Conner 1997). Detections of pileated woodpeckers (mean number detected per 3.5 ha plot sector) were 33% higher (0.85 per plot visit versus 0.64) in infrequently burned pine-hardwood forest habitats than in more regularly burned longleaf pine habitats. Detections of red-bellied woodpeckers and northern flickers were 24% higher (1.56 per plot visit versus 1.26) and 75% higher (0.35 per plot visit versus 0.20), respectively, in pine-hardwood versus open pine habitats. The differences in the abundance of other *Picoides* were even more extreme. Detections of hairy and downy woodpeckers were 350% higher (0.27 per plot visit versus 0.06) and 2300% higher (0.24 per plot visit versus 0.01), respectively, in pine-hardwood versus open pine habitats. In contrast, a mean of 0.46 red-cockaded woodpeckers were detected per plot visit in the open pine habitats whereas none was detected in the pine-hardwood habitats (Shackelford & Conner 1997).

Support for this suggestion that red-cockaded woodpeckers likely were and continue to be a keystone cavity provider for other cavity nesters in well-burned, fire-maintained southern pine ecosystems comes from the abundance of observations of other species using red-cockaded woodpecker cavities. Numerous vertebrate and invertebrate species are known to use red-cockaded woodpecker cavities (Table 1). Because so many other cavity-nesting species are dependent on red-cockaded woodpeckers for cavities, forest biodiversity would suffer substantially in the absence of this endangered woodpecker in fire-maintained pine ecosystems of the South. Several species, such as red-bellied and red-headed woodpeckers and southern flying squirrels appear to compete actively with red-cockaded woodpeckers for intact cavities (Jackson 1978; Neal et al. 1992; Kappes & Harris 1995). The fact that red-

Table 1. Vertebrate and invertebrate species observed using unenlarged and enlarged red-cockaded woodpecker cavities in the southeastern United States.

Cavity occupant	References for observation
Birds	
American kestrel (*Falco sparverius*)	(Rudolph et al. 1990a)
Brown-headed nuthatch (*Sitta pusilla*)	(Jackson 1978)
Carolina chickadee (*Poecile carolinensis*)	(Beckett 1971)
Eastern bluebird (*Sialia sialis*)	(Baker 1971; Jackson 1978)
Eastern screech-owl (*Otus asio*)	(Baker 1971; Conner et al. 1997)
European starling (*Sturnus vulgaris*)	(Dennis 1971; Jackson 1978)
Great crested flycatcher (*Myiarchus crinitus*)	(Baker 1971; Conner et al. 1997)
Northern flicker (*Colaptes auratus*)	(Baker 1971; Dennis 1971)
Pileated woodpecker (*Dryocopus pileatus*)	(Baker 1971; Jackson 1978)
Red-bellied woodpecker (*Melanerpes carolinus*)	(Dennis 1971; Jackson 1978)
Red-headed woodpecker (*M. erythrocephalus*)	(Baker 1971; Beckett 1971)
Tufted titmouse (*Baeolophus bicolor*)	(Baker 1971; Beckett 1971)
White-breasted nuthatch (*Sitta carolinensis*)	(Baker 1971)
Wood duck (*Aix sponsa*)	(Baker 1971)
Mammals	
Eastern gray squirrel (*Sciurus carolinensis*)	(Dennis 1971; Jackson 1978)
Evening bat (*Nycticeius humeralis*)	(Rudolph et al. 1990a)
Fox squirrel (*Sciurus niger*)	(Baker 1971; Jackson 1978)
Raccoon (*Procyon lotor*)	(Loeb 1993)
Southern flying squirrel (*Glaucomys volans*)	(Baker 1971; Beckett 1971)
Reptiles and amphibians	
Broad-headed skink (*Eumeces laticeps*)	(Conner et al. 1997)
Five-lined skink (*Eumeces fasciatus*)	(Jackson 1978)
Gray treefrogs (*Hyla versicolor* & *H. chrysoscelis*)	(Jackson 1978; Conner et al. 1997)
Rat snake (*Elaphe obsoleta*)	(Baker 1971; Dennis 1971)
Arthropods	
Ants	(Conner et al. 1997)
Honey bee (*Apis mellifera*)	(Dennis 1971; Jackson 1978)
Moths (Lepidoptera)	(Conner et al. 1997)
Mud daubers (Sphecidae)	(Conner et al. 1997)
Paper wasps (3 *Polistes* sp.)	(Dennis 1971; Rudolph et al. 1990a)
Spiders	(Conner et al. 1997)

headed and red-bellied woodpeckers, two woodpeckers that normally are primary excavators, regularly use red-cockaded woodpecker cavities for nesting over a wide geographic area (Neal et al. 1992) provides compelling evidence of the keystone role red-cockaded woodpeckers play in upland pine ecosystems. Red-bellied woodpeckers have been reported using red-cockaded woodpecker cavities more than any other species of bird throughout the South.

Pileated woodpeckers enlarge the entrance to red-cockaded woodpecker cavities such that they are no longer useable by the endangered woodpecker (Carter et al. 1989). Red-cockaded woodpeckers likely do not use these enlarged cavities because of their increased vulnerability to predators and competitors. Once a cavity entrance is enlarged, however, larger secondary cavity users, such as the American kestrel, eastern screech-owl, northern flicker, fox squirrel, raccoon, and wood duck, are able to use the cavity (Table 1).

Anthropogenic forces have greatly altered the southern forest landscape over the past 150 years (Frost 1993; Conner et al. 2001a). Exclusion and suppression of fire from fire-maintained ecosystems and conversion of pine forests to other land uses have occurred southwide. Such changes have permitted hardwood species to invade the previously open pine uplands and likely increased the availability of dead trees across the previously pine-dominated landscape. Snags do not always ignite under modern day prescribed fire conditions, especially when nearly all burns are conducted during winter under cool, humid conditions when the risk of wildfire is low. These changes have permitted other species of woodpeckers to be in closer proximity to red-cockaded woodpeckers than they were historically (Saenz et al. 2002). A serious consequence of this change is the high rate of damage done to red-cockaded woodpecker cavities by pileated woodpeckers (Conner et al. 1991; Conner & Rudolph 1995; Saenz et al. 1998; 2002). The rate of damage is so severe that many red-cockaded woodpecker populations suffer an annual net loss of useable cavities. In Texas, red-cockaded woodpecker populations on the Angelina National Forest averaged an annual net loss of 4.6 useable cavities over a 10 year period (Conner et al. 1991; Conner & Rudolph 1995). The loss of cavities to tree death (57 cavity trees) was roughly equal to the loss due to pileated woodpecker enlargement (55 cavity trees).

Red-cockaded woodpeckers could not have evolved in the fire-maintained pine ecosystems of the South if they suffered such a loss rate historically. They would have lost cavities faster than they could have excavated them. Pileated woodpecker abundance and their current rate of cavity destruction likely are elevated above what occurred in the South in the historic fire-maintained pine ecosystems of pre-Columbian times. Testing this hypotheses would be somewhat problematic in present day landscapes. Because of the large home range of a pileated woodpecker pair and red-cockaded woodpecker group, large tracts (5,000+ ha) of unbroken well-burned longleaf pine forest that are not fragmented from a timber-type and land-use perspective and still contained populations of red-cockaded woodpeckers would be needed to test the hypotheses. Such landscape conditions are now only a historic memory (Frost 1993; Conner et al. 2001a).

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FEEDING HABITS OF SONGBIRDS IN EAST TEXAS CLEARCUTS DURING WINTER

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Abstract.—This east Texas study was undertaken to determine the importance of seeds of forbs, grasses, and woody shrubs to songbirds wintering in young pine plantations which had been established utilizing the clearcut regeneration system. The feeding habits and preferences of four species of songbirds, northern cardinals (*Cardinalis cardinalis*), song sparrows (*Melospiza melodia*), dark-eyed juncos (*Junco hyemalis*), and white-throated sparrows (*Zonotrichia albicollis*) were examined from November to February of 1980-81, 1981-82, and 1982-83. Differences in consumption percentages were compared among bird species using *ANOVA* and Duncan's multiple range tests. Paired *t*-tests were used to compare seeds consumed to seeds available by bird species. Differences ($P \leq 0.05$) existed among bird species in consumption percentages of seeds of various genera. Northern cardinals selected seeds of *Callicarpa, Croton, Datura*, and *Galactia*. Song sparrows used seeds of *Ambrosia, Panicum*, and *Seteria* in excess of abundance. Dark-eyed juncos also selected *Ambrosia* as well as *Eragrostis* and *Parietaria* over seeds of other genera. *Ambrosia*, *Parietaria*, *Aristida*, and *Viola* were preferred by white-throated sparrows.

Of the 4.7 million ha of commercial forest land in East Texas, 1.8 million are owned by forest industry (McWilliams & Lord 1988). Most such lands are intensively managed for pine on a short rotation (< 50 years), evenage basis. A common practice on industrial forest lands is to clearcut the marketable timber at rotation age, prepare the site, and plant pine seedlings. After site preparation, growth and seed production of grasses and forbs are stimulated by decreased competition for nutrients, water, and sunlight. In the winter months, seeds of such plants are a valuable food source for birds.

Few data exist on food habits and preferences or food availability to free-ranging songbirds wintering in young southern pine plantations. Therefore, the objectives of this study were to analyze winter foods of northern cardinals (*Cardinalis cardinalis*), song sparrows (*Melospiza melodia*), dark-eyed juncos (*Junco hyemalis*), and white-throated sparrows (*Zonotrichia albicollis*) collected on areas which had been recently clearcut, site prepared, and planted to pine seedlings, and to determine if these species were selecting seeds of certain genera or if their feeding habits were dependent on seed availability.

METHODS

Two study areas in the Pineywoods Ecological Region of east Texas were selected, one in Nacogdoches County and another in Angelina County. Although the areas were in different counties, they were less than 20 km apart. Both areas had been clearcut, then residual vegetation sheared and along with debris, raked into long piles called windrows. The windrows were burned on the Angelina County study area. Both areas were planted with one-year-old pine seedlings during the study period. With one exception, soils on both study areas were well-drained fine sandy loams or loamy sands. A small part of the Angelina County study area was nearly level, thus poorly drained (Worthington 1984).

Northern cardinals, dark-eyed juncos, and song sparrows were collected on the study areas during November, December, January, and February of 1980-81, 1981-82, and 1982-83; white-throated sparrows were collected in 1982-83 only. Efforts were made to collect five individuals of each species on each study area per month. All birds were collected in the morning. Each collected bird was immediately weighed to the nearest 0.5 grams. The digestive tract (esophagus, proventriculus, gizzard) was then removed and injected with 1 CC of 10% formalin (Dillery 1965) to stop the digestive process. The tract was placed in a self-sealing plastic bag along with an identification number. The location where the bird was first observed was marked with plastic flagging bearing the bird's identification number. Upon returning from the field, each digestive tract was frozen and stored.

In the laboratory, the contents of each digestive tract were dried at 38°C for 48 hours, then weighed to the nearest 0.0001 g. Digestive tract contents were then separated into four groups, namely plant seeds, insect parts, grit, or unidentified material. Seeds were then separated to genus using keys (Musil 1963; Landers & Johnson 1976) and a U.S. Forest Service reference seed collection. Seeds not identified were kept separate, labeled unknown, and assigned a number. Many of these unknown seeds were later identified. All food materials were then redried at 38°C for 48 hours and weighed to the nearest 0.0001 g.

Seeds on the ground, presumably available to the collected birds, were sampled during the 1981-82 and 1982-83 study periods, usually the same day the birds were collected. Seeds were sampled on five 10 cm radius subplots in the area where each bird was first observed. The first subplot was where the bird was originally observed and the others were in each cardinal direction, 2 m from the first subplot. Food materials were collected using a hand-held power vacuum. Seeds on standing vegetation directly above the subplots also were collected.

In the laboratory, availability samples were frozen for 48 hours to kill insects, then coarse debris was removed. The remaining material was passed through a series of sieves to sort seeds by size class and remove fine debris. A binocular dissecting scope was used when separating seeds from fine debris. The seeds were sorted, dried, and weighed in the same manner as were seeds in the digestive tracts of the birds. The five subplot samples were combined to form a single availability sample for analyses.

For each bird species, the number of individuals that consumed each seed genus was determined by study area. Each value was then divided by the total number of birds of that species to obtain frequency of occurrence. Differences in frequencies of occurrence were tested among bird species by study area using two-by-four Chi-square tests.

Due to differences in body weights and total digestive tract content weights among the four bird species (Worthington 1984:61), actual weights of seed genera consumed were not compared among the bird species. Instead, weights of all identified and unidentified seeds in each bird's digestive tract were summed and the weight of each genus was converted to a percent of that sum. These values reflected consumption percentages and were compared among the four bird species. Seeds available to the birds were evaluated similarly. The conversion of actual weights to percentages also allowed for comparisons between consumed and available seeds. Insect parts, grit, and unidentified material were not compared.

Differences among bird species in seed consumption percentages were tested using *ANOVA* with Duncan's multiple range tests. Differences in seed availability percentages were tested in the same manner. For each genus, paired *t*-tests were used to compare percentages of seeds consumed to percentages of seeds available by bird species and study area. As seed availability data were not collected in 1980-81, seed consumption data from that year were not used when comparing seeds consumed to those available.

In order for a seed genus to be included in the statistical comparisons of digestive tracts, it had to average at least 2% of consumed seeds, by weight, for at least one bird species. To be included in comparisons of availability data, a genus had to comprise at least 4% of the available seeds, by weight, for at least one bird species. Throughout the study, the null hypothesis used was that of no difference among groups being tested. The rejection level was set at 0.05 for all tests.

RESULTS

Ninety-five northern cardinals, 59 song sparrows, and 86 dark-eyed juncos were collected during the three winters; 45 white-throated sparrows were collected in the winter of 1982-83. Unidentified material comprised 64.2, 67.0, 65.7, and 72.9% of weights of digestive tract contents of northern cardinals, song sparrows, dark-eyed juncos, and white-throated sparrows, respectively; identifiable seeds made up 23.5, 16.5, 18.2, and 14.3% of digestive tract content weights of the four species, respectively. With one exception, small amounts of greenery, insects, and grit made up the remainder; one northern cardinal had consumed a ground skink *(Scincella lateralis)*. Most unidentified material was in the gizzard. It was assumed that proportions of unidentifiable material in that organ were the same as those identifiable (West 1973).

Seeds consumed.—Seeds of 38 genera were identified and recorded in digestive tracts of the birds (Worthington 1984:64-74). Eight groups of seeds could not be identified, but only one was consumed in greater than trace (i.e., < 1.0%) quantities. With one exception, seeds of all identifiable genera recorded in digestive tracts were also recorded in availability samples; no *Datura* seeds were recorded in availability samples.

In Nacogdoches County, differences existed among bird species in frequencies of occurrence of seeds of 10 genera (Table 1). A higher proportion of the northern cardinal digestive tracts contained seeds of *Callicarpa, Croton,* and *Datura* than did those of the other three bird species. Conversely, *Ambrosia* occurred in a lower proportion of northern cardinals than in the other three species. *Eragrostis* and

Table 1. Numbers of birds and frequency of occurrence of seeds in digestive tracts of northern cardinals (NOCA), song sparrows (SOSP), dark-eyed juncos (DEJU), and white-throated sparrows (WTSP, 1982-1983 only) collected in eastern Texas during winter 1980-81, 1981-82, and 1982-83. Within a row, a different letter indicates different frequencies of occurrence among bird species at the 0.05 level.

Seed genera	NOCA		SOSP		DEJU		WTSP		X^2
	n	%	*n*	%	*n*	%	*n*	%	*P*
NACOGDOCHES COUNTY									
Amaranthus	7	12.3a	2	18.2a	24	51.1b	5	23.8a	<0.001
Ambrosia	4	7.0a	5	45.5b	26	55.3b	15	71.4b	<0.001
Callicarpa	23	40.4a	1	9.1b	0	0.0b	2	9.5b	<0.001
Carex	4	7.0	1	9.1	0	0.0	0	0.0	0.153
Croton	28	49.1a	0	0.0b	0	0.0b	1	4.8b	<0.001
Cyperus	2	3.5a	3	27.3b	8	17.0b	0	0.0a	0.008
Datura	29	50.1a	2	18.2b	3	6.4b	0	0.0b	<0.001
Digitaria	12	21.1	4	36.4	13	27.7	1	4.8	0.120
Eragrostis	0	0.0a	5	45.5c	12	25.5b	0	0.0a	<0.001
Panicum	2	3.5a	6	54.6c	11	23.4b	0	0.0a	<0.001
Parietaria	0	0.0a	1	9.1a	20	42.6b	12	57.1b	<0.001
Paspalum	4	7.0	2	18.2	2	4.3	0	0.0	<0.201
Phytolacca	20	35.1a	2	18.2ab	3	6.4b	0	0.0b	<0.001
Rudbeckia	0	0.0	0	0.0	2	4.3	0	0.0	<0.284
Sample size	57		11		47		21		
ANGELINA COUNTY									
Amaranthus	0	0.0a	2	4.2a	12	30.8b	1	4.5a	<0.001
Ambrosia	4	10.5a	15	31.3b	17	43.6b	12	50.0b	0.003
Callicarpa	14	36.8a	0	0.0b	0	0.0b	0	0.0b	<0.0001
Carex	12	31.6a	16	33.3a	1	2.6b	4	16.7b	0.002
Croton	13	34.2a	1	2.1b	1	2.6b	0	0.0b	<0.001
Cyperus	1	2.6a	8	16.7ab	10	25.6b	6	25.0b	0.031
Datura	15	39.5a	3	6.3b	0	0.0b	0	0.0b	<0.001
Digitaria	0	0.0a	7	14.6b	7	18.0b	1	4.5ab	0.029
Eragrostis	0	0.0	3	6.3	4	10.3	1	4.5	0.252
Panicum	1	2.6a	38	79.2b	31	79.5b	8	33.3c	<0.001
Parietaria	0	0.0	1	2.1	1	2.6	0	0.0	0.693
Paspalum	2	5.3a	2	4.2a	8	20.5b	0	0.0a	0.008
Phytolacca	0	0.0	4	8.3	2	5.1	0	0.0	0.172
Rudbeckia	0	0.0a	1	2.1a	10	25.6b	0	0.0a	<0.001
Sample size	38		48		39		24		

Panicum seeds were found in greater proportions of song sparrow digestive tracts than in those of the other three species and in more dark-eyed junco tracts than in northern cardinal or white-throated sparrow tracts. *Amaranthus* occurred in a higher proportion of dark-eyed juncos than in the other three bird species. A majority of white-throated sparrows consumed *Ambrosia* and *Parietaria.*

In Angelina County, *Callicarpa*, *Croton,* and *Datura* were recorded in higher proportions of northern cardinal digestive tracts than in those of the other three species (Table 1). Conversely, *Ambrosia* and *Panicum* were found in lower proportions of northern cardinal digestive tracts than in digestive tracts of the other species. *Ambrosia* was found in half of white-throated sparrows, and *Panicum* occurred in almost 80% of the song sparrows and dark-eyed juncos. Finally, higher proportions of dark-eyed juncos than the other species consumed *Amaranthus, Paspalum,* and *Rudbeckia.*

Seeds of 23 genera comprised at least 2% of the total weight of seeds in the digestive tracts of one or more bird species (Worthington 1984:64-74). Percent consumption of 12 of these genera differed among bird species (Table 2). Combined, *Croton* and *Datura* comprised approximately 64 and 43% of the weight of seeds in the digestive tracts of northern cardinals collected on the Nacogdoches County and Angelina County study areas, respectively. On both study areas, these combined percentages were higher than those of the other three bird species (Table 2). Song sparrows and dark-eyed juncos consumed relatively large quantities of *Ambrosia, Digitaria,* and *Panicum* on both study areas. Percent consumption of these genera by song sparrows and dark-eyed juncos were generally higher than for northern cardinals and white-throated sparrows, except for *Ambrosia* which made up a higher percentage of the digestive tract contents of white-throated sparrows than of the other species (Table 2). On the Nacogdoches County study area, white-throated sparrows also consumed relatively more *Parietaria* than did the other species.

Seeds available.—Eighty-two genera of seeds were collected on the two study areas, 72 on the Nacogdoches County study area and 61 on the Angelina County study area (Worthington 1984:62-63). Fifty-one genera were common to both areas; 21 and 10 were exclusive to Nacogdoches County and Angelina County, respectively. However,

Table 2. Weights (in percent) of seeds recorded in digestive tracts of northern cardinals (NOCA), song sparrows (SOSP), dark-eyed juncos (DEJU), and white-throated sparrows (WTSP, 1982-1983 only) collected in eastern Texas during winter 1980-81, 1981-82, and 1982-83. Only genera for which there were significant differences among bird species are shown. Within a row by study area, a different letter denotes different proportions among bird species at the 0.05 level.

	Nacogdoches County				Angelina County			
Seed genera	NOCA	SOSP	DEJU	WTSP	NOCA	SOSP	DEJU	WTSP
Amaranthus	0.39a	2.07ab	26.46c	13.30b	0.00a	1.43a	10.50b	3.72ab
Ambrosia	0.35a	24.94b	26.42b	49.05c	4.18a	11.64a	9.98a	39.41b
Callicarpa	8.08a	4.55ab	0.00b	1.99b	17.21a	0.00b	0.00b	0.00b
Carex	1.28	0.79	0.00	0.00	5.58ab	10.18b	1.87a	4.48ab
Croton	34.40a	0.00b	0.00b	2.94b	21.00a	1.50a	0.93b	0.00b
Datura	30.04a	2.29b	0.65b	0.00b	22.50a	0.44b	0.00b	0.00b
Digitaria	0.30a	15.24b	8.12b	1.14a	0.00a	0.92ab	3.31b	0.80ab
Eragrostis	0.00a	7.01b	5.50b	0.00a	0.00	1.25	0.74	0.11
Panicum	0.07a	6.50b	3.84b	0.00a	0.27a	42.74b	34.81b	13.91a
Parietaria	0.00a	8.54ab	15.34b	28.05c	0.00	1.35	0.55	0.00
Paspalum	1.99	6.79	1.91	0.00	0.25a	1.07a	7.10b	0.00a
Phytolacca	11.53a	10.67a	1.53b	0.00b	0.00	3.28	1.40	0.00
Total (%)	88.44	89.39	89.77	96.47	71.26	75.80	71.19	62.43
Sample size	57	11	47	21	38	48	39	24
							0.55	0.00

only 16 genera each contributed a minimum of 4% of the seeds available to at least one bird species.

The genera of frequently occurring seeds included *Andropogon, Digitaria, Panicum, Phytolacca, Rhus, Solidago,* and *Uniola.* On the Nacogdoches County study area, there were differences among bird species in seed availability frequencies of five commonly occurring genera (Worthington 1984:34). However, only *Ambrosia, Digitaria,* and *Eragrostis* comprised at least 2% of the weight of seeds consumed. *Ambrosia* occurred more frequently in white-throated sparrow and song sparrow food availability samples than in those of northern cardinals, and *Digitaria* was recorded in higher percentages of song sparrow and dark-eyed junco than white-throated sparrow food availability samples. *Eragrostis* was found in a higher percentage of song sparrow food availability samples than in those of the other species (Worthington 1984:34). For the Angelina County study area, frequencies of only two seed genera differed among food availability samples (Worthington 1984:35). Neither of these, *Eupatorium* and *Heterotheca*, could be considered important food items to the collected birds.

Table 3. Weights (in percent) of seeds available to northern cardinals (NOCA), song sparrows (SOSP), dark-eyed juncos (DEJU), and white-throated sparrows (WTSP, 1982-1983 only) collected in eastern Texas during winter 1981-82 and 1982-83. Genera shown are those for which there were differences in percent availability and/or percent consumption. Within a row by study area, a different letter denotes different proportions at the 0.05 level.

	Nacogdoches County				Angelina County			
Seed genera	NOCA	SOSP	DEJU	WTSP	NOCA	SOSP	DEJU	WTSP
Amaranthus	8.78a	4.54a	25.92c	17.28b	0.56	3.11	3.40	1.64
Ambrosia	0.89	3.13	4.36	3.51	0.14a	5.79ab	8.25b	1.31ab
Callicarpa	7.68	6.21	3.74	1.81	2.30	0.10	0.00	0.79
Carex	0.02	0.00	0.03	0.00	0.09	4.27	0.47	3.32
Croton	4.95	0.49	4.74	1.65	0.30	0.02	0.24	0.51
Digitaria	1.13a	14.23b	3.41a	0.31a	0.00a	0.34a	1.96b	0.49a
Eragrostis	0.15	0.75	0.26	0.00	1.09	0.71	0.13	3.08
Eupatorium	1.69	3.25	0.52	2.06	2.33	7.90	1.88	3.89
Galactia	0.28a	5.94b	1.25a	0.65a	0.00	0.17	0.00	0.00
Heterotheca	0.95	5.01	1.28	3.18	7.72	2.29	6.96	12.83
Panicum	5.18	7.74	2.63	0.44	10.54a	25.99b	26.00b	11.02a
Parietaria	0.00	0.21	0.10	0.35	0.00	0.00	0.00	0.00
Paspalum	0.74	0.93	0.06	0.17	1.57	0.92	0.00	1.28
Phytolacca	14.16a	5.33a	10.30a	30.11b	1.13	2.17	2.43	0.18
Rhus	29.26	33.77	21.88	28.93	21.75a	5.14b	15.94ab	24.42a
Uniola	0.43	0.00	0.63	0.64	7.28	9.42	9.56	8.26
Sample size	42	7	37	21	29	39	24	24

There were some differences in weights (in percent) of seeds available to the bird species in each county (Table 3). In Nacogdoches County, there were differences among species for *Amaranthus, Digitaria, Galactia*, and *Phytolacca*. There was a higher proportion of *Amaranthus* seeds in dark-eyed junco availability samples than in those of the other species, and a higher proportion in white-throated sparrow samples than in northern cardinal or song sparrow samples. Song sparrow availability samples contained higher proportions of *Digitaria* and *Galactia* seeds than did samples for the other species, and *Phytolacca* seeds ranked higher in white-throated sparrow samples than in samples for the other species (Table 3).

In Angelina County, there were differences in seed availability percentages of *Ambrosia, Digitaria, Panicum*, and *Rhus* among bird species. Both *Ambrosia* and *Panicum* seeds were less available to northern cardinals than to the other species. *Digitaria* seeds ranked higher for dark-eyed juncos than for the other species, but made up less than 2% of the food available to that species. *Rhus,* which comprised large proportions of the seeds available on both study areas (Table 3), was not an important food source to any species.

Seeds selected.—Callicarpa, Croton, Datura, Galactia, and *Phytolacca* comprised 90% of the seeds consumed by northern cardinals in Nacogdoches County during the winters of 1981-82 and 1982-83 (Table 4); *Croton, Datura,* and *Galactia* were consumed in excess of availability. The same was true of *Callicarpa* and *Croton* in Angelina County. *Phytolacca* availability exceeded consumption in Nacogdoches County but was not recorded in any Angelina County digestive tracts (Table 4).

Only seven song sparrows were collected in Nacogdoches County, thus statistical comparisons are weak at best. However, almost 35% of the seeds identified in the digestive tracts of those birds were *Ambrosia.* Seeds of that genus, *Carex, Panicum,* and *Seteria* were dominant in Angelina County song sparrows. Consumption percentages of the two latter genera were greater than availability percentages (Table 4).

For darked-eyed juncos from Nacogdoches County, consumption of *Ambrosia, Eragrostis,* and *Parietaria* exceeded availability. *Amaranthus,* which was readily available on that study area, comprised slightly over 25% of the seeds consumed. In Angelina County, seeds of *Amaranthus, Ambrosia, Digitaria,* and *Panicum* comprised almost 70% of identifiable seeds in dark-eyed junco digestive tracts; consumption and availability percentages of these genera were similar (Table 4).

White-throated sparrows were collected only in 1982-83. In both counties, *Ambrosia* compromised the largest proportion of identifiable seeds. Consumption of that genus and *Parietaria* exceeded availability in Nacogdoches County. In Angelina County, *Ambrosia, Aristida,* and *Viola* demonstrated similar trends. *Amaranthus* in Nacogdoches County and *Cyperus* and *Panicum* in Angelina County were important food items for which consumption and availability percentages did not differ (Table 4). *Rhus* seeds were recorded in two white-throated sparrows in Angelina County.

DISCUSSION

Although identifiable seeds comprised relatively small proportions of digestive tracts, this study provided strong evidence that northern cardinals, song sparrows, dark-eyed juncos, and white-throated sparrows

Table 4. Comparisons of percent seed availability and percent seed consumption for northern cardinals, song sparrows, dark-eyed juncos, and white-throated sparrows in eastern Texas during winter 1981-82 and 1982-83. Paired *t*-tests values also are shown.

	Nacogdoches County			Angelina County		
Seed genera	Pct. Avail.	Pct. Cons	*P* - value	Pct. Avail.	Pct. Cons.	*P* - value
Northern cardinals			$n = 42$			$n = 29$
Amaranthus	8.78	0.19	0.006	0.57	0.00	0.194
Callicarpa	7.68	9.22	0.481	2.63	19.09	0.030
Carex	0.02	1.91	0.230	1.03	6.36	0.162
Croton	4.95	46.01	<0.001	0.31	26.81	0.001
Datura	0.00	24.35	<0.001	0.00	6.66	0.113
Galactia	0.28	5.16	0.041	0.00	0.00	1.000
Heterotheca	0.95	0.01	0.049	7.69	0.00	0.047
Myrica	2.17	0.00	0.274	5.16	0.00	0.153
Panicum	5.18	0.03	0.018	10.77	0.33	0.024
Phytolacca	14.16	5.31	0.016	1.15	0.00	0.179
Rhus	29.26	0.00	<0.001	22.92	0.00	0.002
Uniola	0.43	0.00	0.310	7.91	3.66	0.381
Song sparrows			$n = 7$			$n = 39$
Amaranthus	4.54	0.87	0.252	3.11	1.77	0.615
Ambrosia	3.28	34.91	0.053	5.79	11.41	0.227
Carex	0.00	1.23	0.356	4.27	8.47	0.265
Digitaria	14.23	19.29	0.734	0.34	0.49	0.880
Eupatorium	3.25	0.00	0.352	7.90	0.00	0.001
Panicum	7.74	2.15	0.343	25.99	44.48	0.010
Phytolacca	5.33	0.00	0.120	2.17	2.60	0.894
Rhus	33.74	0.00	0.071	5.14	0.00	0.042
Seteria	0.00	0.00	1.000	0.00	6.35	0.044
Uniola	0.00	0.00	1.000	9.42	0.03	0.004
Dark-eyed juncos			$n = 37$			$n = 24$
Amaranthus	26.10	25.63	0.912	3.40	11.27	0.110
Ambrosia	4.33	29.60	<0.001	8.25	13.88	0.454
Digitaria	3.37	5.93	0.337	1.96	5.25	0.312
Eragrostis	0.27	5.62	0.044	0.13	1.12	0.169
Heterotheca	1.29	0.00	0:049	6.96	0.00	0.035
Panicum	2.63	3.37	0.641	25.95	39.23	0.166
Parietaria	0.10	19.49	<0.001	0.00	0.89	0.094
Phytolacca	10.20	0.30	<0.001	2.43	2.28	0.658
Rhus	21.75	0.00	<0.001	15.91	0.00	0.025
Uniola	0.63	2.28	0.135	9.54	2.22	0.117
White-throated sparrows*			$n = 21$			$n = 24$
Amaranthus	17.28	13.30	0.645	1.64	3.72	0.637
Ambrosia	3.51	49.05	<0.001	1.31	39.41	0.001
Aristida	0.00	0.00	1.000	0.00	11.99	0.041
Cyperus	0.13	0.00	0.892	3.20	8.88	0.409
Eupatorium	2.06	0.00	0.134	3.89	0.00	0.106
Heterotheca	3.18	0.14	0.181	12.83	0.00	0.016
Panicum	0.44	0.00	0.014	11.02	13.91	0.948
Parietaria	0.35	28.05	0.002	0.00	0.00	1.000
Phytolacca	30.11	0.00	<0.001	0.18	0.00	0.319
Rhus	28.93	0.00	0.001	24.42	1.28	0.008
Uniola	0.64	0.00	0.329	8.26	0.40	0.057
Viola	0.00	2.35	0.126	0.00	6.28	0.020

* Collected in winter 1982-83 only.

selected seeds of some genera over those of others. Korschgen (1980) noted that if a food item occurred in high numbers of individuals and in high volume within the individuals, the food was of high quality or preference. In this study, three or four genera met these criteria for each bird species. For most of these genera, consumption exceeded availability.

Seeds utilized by northern cardinals were very different from those used by the other species. With study areas combined, *Callicarpa, Croton,* and *Datura* comprised approximately 69% of the seeds identified in northern cardinal digestive tracts. These genera made up only trace proportions in digestive tracts of the other bird species. The importance of *Croton* and *Callicarpa* to northern cardinals is well-documented (Martin et al. 1951; Halkin & Linville 1999). *Carex, Rhus, Setaria,* and *Panicum* have also been classified as important to northern cardinals (Halkin & Linville 1999). Although seeds of these genera were collected on the study areas, they made up minor portions of northern cardinal diets, and no *Rhus* was recorded in any northern cardinal. No mention of northern cardinals consuming *Datura* was found in the literature. Reasons for the absence of *Datura* seeds in availability samples are unknown; *Datura* plants were present on both study areas.

Although there were similarities in diets of song sparrows, dark-eyed juncos, and white-throated sparrows, the relative rank of the important genera varied among species. For song sparrows, *Panicum* made up 38% of identifiable seeds; *Ambrosia* (15%) ranked second and *Carex* (7%) third. Neither Martin et al. (1951) nor Arcese et al. (2002) listed *Panicum* as an important food source for song sparrows. Results of this study contradict those findings, and it is possible that the low number of song sparrows collected in Nacogdoches County was due to the lack of *Panicum*. *Ambrosia* seeds are an important winter food item for song sparrows (Martin et al. 1951), as are those of *Amaranthus, Digitaria,* and *Setaria* (Arcese et al. 2002). In this study, seeds of these three genera comprised relatively minor proportions of song sparrows diets.

In dark-eyed junco digestive tracts, *Ambrosia* (23%), *Amaranthus* (20%), *Panicum* (18%), and *Parietaria* (12%) made up almost three-fourths of the identifiable seeds. Judd (1901) and Nolan et al. (2002) noted the importance of *Ambrosia* and *Amaranthus* to dark-eyed juncos.

Martin et al. (1951) also found seeds of *Ambrosia* and various grasses to be important food items for the species.

White-throated sparrows were abundant on both study areas during winter 1982-83. With data from study areas pooled, *Ambrosia,* (43%) comprised a higher proportion of that species diet than did any genera in diets of the other species. Falls & Kopachena (1994) noted the importance of *Ambrosia* to white-throated sparrows. However, they also stated that fruits of *Rhus* were important to the species. During this study, numerous white-throated sparrows were observed foraging in *Rhus*, and it was assumed that they were eating *Rhus* fruit. Several of those were birds were collected, yet *Rhus* seeds comprised a very minor proportion of the diet. Halls (1977) noted that birds cannot sustain weight on a heavy diet of *Rhus* and that it is normally eaten with other foods. The very small amount of *Rhus* consumed by birds collected in this study support Halls' comments and indicate that birds observed foraging in *Rhus* were either seeking other food items or were consuming minute quantities of that genus.

CONCLUSIONS

In this study, each bird species consumed seeds of several genera in excess of availability. Also, availability percentages exceeded consumption percentages for some genera and did not differ for others. Although seeds of all genera were available to each species, the differences among species may have been due to differences in habitat selection within the clearcuts. Virtually all northern cardinals were first observed in or adjacent to the relatively dense vegetation of the windrows or small riparian zones which were present on both study areas. Song sparrows were usually in dense grassy areas between rows of planted pine seedlings. Dark-eyed juncos were in similar areas, but at higher elevations where ground cover was less dense. White-throated sparrows were collected in areas similar to those of northern cardinals. These results demonstrate that when properly administered, the clearcutting method of regeneration creates excellent habitat for ground-foraging, seed-eating birds which winter in the southern United States. This method creates openings in the forest and, combined with site preparation techniques that scarify both the soil and dormant seeds, promotes the establishment of seed-bearing forbs and grasses.

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INDEX TO VOLUME 56 (2004)
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This index has separate subject and author sections. Words, phrases, locations, proper names and the scientific names of organisms are followed by the initial page number of the article in which they appeared. The author index includes the names of all authors followed by the initial page number of their respective article(s).

SUBJECT INDEX

AUTHOR INDEX

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Allison, T.
Anderson, J.
Arnold, K.
Baskin, J.
Bestgen, K.
Bidwell, T.
Bray, S
Breshears, D.
Brush, T.
Bryan, Jr, A.
Burk, J.
Cameron, G.
Cecil, D.
Ciccimuri, D.
Clark, W.
Connor, W.
Cook, T.
Curran, S.
Dinsmore, S.
Divine, D.
Ernst, C.
Everitt, J.
Farrish, K.
Foster, C.
Gelwick, F.
Graves, J.
Harcombe, P.
Harper, C.
Harper, D.
Harrel, R.
Harveson, L.
Hathcock, C.
Henke, S.
Henry, B.
Hicks, D.
Highton, R.
Holley, A.
Howells, R.
Hurst, G.
Jones, R.
Judd, F.
Jurena, P.
Krauss, K.
Lonard, R.
MacFadden, B.
Mathewson, C.
Maxwell, T.
McAllister, C.
McDonald, H.
McGregor, K.
Monfredo, W.
Montagna, P.
Murray, H.
Nieland, D.
Norwine, J.
Ortego, B.
Painter, C.
Parker, W.
Persans, M.
Rayor, L.
Ribble, D.
Richardson, A.
Riskind, D.
Robertson, P.
Rupert, J.
Schmidlin, T.
Schwertner, T.
Schwimmer, D.
Siemann, E.
Singer, F.
Smeins, F.
Smith, E.
Stangl, Jr., F.
Taylor, E.
Upton, S.
Wake, D.
Walker, E.
Wallace, M.
Walley, H.
Welbourn, W.
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Woodin, M
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