

**FINAL REPORT**

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Endangered and Threatened Species Conservation

**WER42: Historical and Local Processes Determining the Current  
Status of *Macrocllemys tesnminckii*: the Alligator  
Snapping Turtle in Texas**

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## FINAL REPORT

STATE: Texas

GRANT NO: E-1-13

PROGRAM TITLE: Endangered and Threatened Species Conservation

PERIOD COVERED: September 1, 1998 - August 31, 2001

PROJECT NUMBER: WER42

PROJECT TITLE: Historical and Local Processes Determining the Current Status of *Macrolemys temminckii*: the Alligator Snapping Turtle in Texas.

### SEGMENT COST:

TOTAL - \$48,131.10

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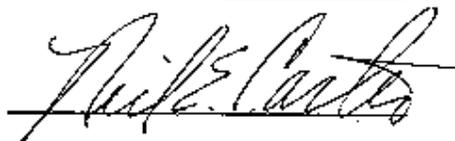
### PROJECT OBJECTIVES:

1. To conduct a survey of the existing range of the alligator snapping turtle in Texas from an intensive trapping program, questionnaires, and specimen records in the literature and museums.
2. To collect basic data on museum specimens from Objective 1, including sex, age, size, reproductive condition, and cause of mortality when it can be discerned from the specimen.
3. To conduct a telemetry study of alligator snapping turtles.
4. To provide a continuous account of ambient and body temperatures of the turtle being monitored using miniature temperature data loggers.
5. To measure water quality variables at microhabitat sites determined by radio telemetry and at random sites in the same habitat.

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03/18/02

APPROVED BY:



03/21/02

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Date

**HISTORICAL AND LOCAL PROCESSES DETERMINING THE CURRENT  
STATUS OF *MACROCLEMYS TEMMINCKII*, THE ALLIGATOR SNAPPING  
TURTLE IN TEXAS**

**FINAL REPORT  
PROJECT WER42**

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## INTRODUCTION

The Alligator Snapping Turtle (*Macrolemys temminckii*) is distributed from the Suwannee River drainage in northern Florida to the Brazos River drainage in Texas and north in the major river drainages to Kansas, Iowa, and Illinois (Conant and Collins 1991; Pritchard 1989; Roman et al. 1999). The species is highly aquatic and restricted to river systems and their associated bodies of water. With the exception of nesting females, Alligator Snapping Turtles rarely leave aquatic habitats (Harrel et al. 1996; Sloan and Taylor 1997). A recent phylogeographic study using molecular data demonstrated that populations of *Macrolemys temminckii* are genetically differentiated among river drainages (Roman et al. 1999). Roman et al. (1999) hypothesized that the highly aquatic behavior and resultant limited dispersal between drainages caused restricted genetic interchange between river basins. Molecular evidence indicated subdivision of the population into three major lineages (Roman et al. 1999). In their analysis, *Macrolemys temminckii* from the Suwannee River drainage were a distinct clade, and populations from drainages in the Florida Panhandle were grouped into a clade from the central part of the species' distribution. The geographically widespread western lineage includes populations from the Mississippi River and from the Trinity and Neches Rivers in Texas (Roman et al. 1999). A paucity of additional genetic structuring within this lineage suggests relatively recent colonization of this area following Pleistocene climatic fluctuations, a pattern common among many aquatic taxa in the region (Roman et al. 1999).

The Alligator Snapping Turtle is among the largest freshwater turtles with records exceeding 100 kg (Pritchard 1989). Males reach larger sizes than females with a maximum recorded median carapace lengths of 71.1 cm and 57.0 cm respectively (Pritchard 1989). Sexual maturity is reached at median carapace lengths of approximately 37 cm and 33 cm for males and females respectively (Dobie 1971). Alligator Snapping Turtles inhabit a wide variety of permanent aquatic habitats including river channels, lakes and reservoirs, marshes, bayous, and wooded swamps (Sloan and Taylor 1987; Pritchard 1989; Harrel et al. 1996). Alligator Snapping Turtles have a life history characteristic of a long-lived, late-maturing species. Reproductive output is relatively low; sexual maturity is attained in 11-13 years, females lay a single clutch of eggs each year that they reproduce, and clutch size ranges from 16-52 (Dobie 1971; Pritchard 1989). Frequency of reproduction is very difficult to study in Alligator Snapping Turtles, but Pritchard (1989) cited Dobie's data on examination of reproductive tracts, and implied females may nest in alternate years. Growth is rapid, but variable, for immatures and slows considerably with the attainment of sexual maturity (Dobie 1971). Alligator Snapping Turtles are long-lived, with maximum recorded ages of 36 years in the field and 58 years in captivity (Conant and Hudson 1949; Dobie 1971).

Numerous authors have expressed concern about the conservation status of Alligator Snapping Turtles. Pritchard (1989) summarized the known information on the status of Alligator Snapping Turtles and concluded that the species was depleted in most states. Most states, including Texas, have given protection to Alligator Snapping Turtles. However, Louisiana still has a commercial industry that may impact adjacent states (Wagner et al. 1996).

The purpose of this study was two-fold. The first objective was to determine the current distribution (presence/absence) of Alligator Snapping Turtles in Texas. This was accomplished by documenting presence or absence of the species at each survey site using a standardized protocol of setting hoop traps. We selected sites in suitable habitat in the major drainages from the Red River in the north to the Brazos River in the southwest. The second objective was to characterize a population of Alligator Snapping Turtles at selected study sites, and investigate patterns of habitat use, habitat selection, and general activity and movement patterns of Alligator Snapping Turtles.

## METHODS

### Alligator Snapping Turtle Survey

Sampling was conducted using 1.2 m diameter hoop nets consisting of 3-5 hoops and 24 mm mesh. Traps were baited with approximately 0.5 kg of fresh fish (whole or large portions). A series of 15 traps were set at each site and operated for 3 days. Traps were checked daily, all turtles removed and recorded, and bait replaced. Traps were set in water deeper than 1 m, and arranged so that a portion was above water to allow trapped animals to breathe. Occasionally, trap days were lost due to theft, destruction by large alligators, or rapid change in water levels.

All species of turtles captured were weighed, mean carapace length measured, and gender determined prior to release at the point of capture. In addition, a 2 ml blood sample was taken from the caudal vein of all turtles and deposited at the Texas Cooperative Wildlife Collection, Texas A&M University. These samples are available to the scientific community for future research. Alligator Snapping Turtles were permanently marked using stainless steel pan-head screws placed in the rear marginals of

the carapace. Each marginal corresponded to a specific number, and by marking different combinations of marginal scutes, each turtle was assigned a unique identification number.

Historical localities of Alligator Snapping Turtles were obtained from natural history collections and from the literature to determine the extent of the historical range in the state. We also produced a brochure/questionnaire that was distributed to individuals thought to have a reasonable probability of encountering Alligator Snapping Turtles (e.g., Texas Parks and Wildlife Department employees, U. S. Forest Service employees, wildlife professionals). Resulting reports of Alligator Snapping Turtles were collated to provide additional information on the distribution of the species in Texas.

Habitat data were collected at each trap location. Water depth at trap location, maximum channel depth, width of aquatic habitat, and distance to shore were measured (m) for each trap site. Turbidity (Seichi disk), and temperatures at the surface and bottom of the water column were recorded. Substrate type (mud, sand, gravel, rock, detritus); structure type (submerged vegetation, floating vegetation, logs, roots, overhanging branches, bank undercut, none); and structure amount (none, sparse common, abundant) were also recorded. Distance to nearest canopy tree (m), species of nearest tree, and canopy closure (%), were also determined. Within a 5 m radius plot coverage of submerged vegetation (%), floating vegetation (%), and the number of woody stems were recorded. The number of trotlines (active and abandoned) that were present, within the length of the channel subject to trapping, were also recorded.

#### TELEMETRY, POPULATION, AND HABITAT STUDIES

We selected two sites for population, movement, and habitat studies: Bingham Lake in Tyler Co., and Bonaldo Creek in the Stephen F. Austin Experimental Forest. At

Bingham Lake we concentrated on characterizing the population and quantifying habitat use based on microhabitat variables and temperature. At the Bonaldo Creek site, we monitored telemetered individuals in the creek to gather data on the general movement and activity patterns of Alligator Snapping Turtles in a small stream system.

*Telemetry Study at Bonaldo Creek, Stephen F. Austin Experimental Forest*

Alligator Snapping Turtles were trapped in Bonaldo Creek at the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas. Bonaldo Creek, at the study site, is an intermittent to small permanent stream that meanders across the floodplain of the Angelina River. The vegetation of the floodplain consists of mature bottomland hardwood forest dominated by *Quercus* spp., *Carya* spp., *Nyssa sylvatica*, *Betula nigra*, and *Liquidambar styraciflua*.

Five turtles were fitted with radio-transmitters and relocated as time allowed. Relocation points were recorded using GPS. At each relocation point, habitat data were recorded with the same protocol used in the geographic distribution study. Similar habitat data were also collected at random points within the collective home ranges of the five telemetered turtles.

This portion of the study is still in progress, and will continue until the current transmitters battery life is expended.

*Telemetry, population, and Habitat studies at Bingham Lake*

Bingham Lake is an oxbow lake of the Neches River, Tyler Co., Texas, isolated from the river by an earthen dam. The lake is 3.4 km long and ranges in width from 10 to 76 m with sharply sloped banks, a mean depth of 2.4 m, and a maximum depth of 5.4 m. Water level of the lake fluctuated <1.5 m during the study. The lake was acidic, stained,

and turbid because of large amounts of leaves and vegetation accumulated on the lake bottom. Herbaceous vegetation was sparse and consisted of duckweed (*Lemna sp.*), mosquito fern (*Azolla caroliniana*), watermilfoil (*Myriophyllum spicatum*) and occasional mats of water lily (*Nuphar sp.*). Woody vegetation included bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), river birch (*Betula nigra*), and wax myrtle (*Myrica cerifera*).

### Trapping and Marking

*Macrolemys temminckii* were captured and marked with the same methods used in geographic distribution surveys. At Bingham Lake, captured turtles were sexed, weighed, and five morphological characters measured: straight-line carapace length, maximum carapace length, carapace width, maximum depth of shell, and skull width.

### Population Estimates

Recapture data were used to estimate population size using the joint hypergeometric maximum likelihood estimator (JHE) and the NOREMARK (White 1996) computer program. This method of population estimation assumed all marked animals were present for each survey and the population was geographically and demographically closed. These assumptions were valid because Bingham Lake was isolated from other water bodies. We never observed *M. temminckii* on land, and 11 telemetered animals did not leave the site over a 2 year period. Other studies also showed *Macrolemys temminckii* essentially never move overland (Sloan and Taylor 1987, Harrell et al. 1996).

### Habitat Selection

Eleven turtles were fitted with external radio transmitters (16M, Advanced Telemetry Systems, Isanti, MN, weight = 29 g). Telemetered turtles were relocated using a multi-channel radio receiver (TR2, Telonics, Mesa, AZ) and a two-element yagi antenna. We verified accuracy of locations at the beginning of the study by probing with a pole until we hit the turtle and it moved. Turtles were usually within 1 m of radiotelemetered locations. Telemetered turtles were relocated six times per month.

We tested the null hypothesis that turtles did not select microhabitat sites by comparing microhabitat variables measured at occupied sites (OS) to the same suite of variables measured at paired, random sites (RS) available to them. For each measured occupied site (OS) we chose paired random sites (RS). This method randomly chooses sites that were available to the individual turtle at the same time, but that were not occupied. Random sites were chosen using two random numbers generated from the uniform distribution. The first random number dictated linear stream distance (m) from OS, while the second dictated the percentage of distance across the oxbow. The distance from OS to RS was constrained to between 4 and 100 m. Distances < 4 m were eliminated because in some cases, such as when turtles were beneath large submerged logs, short distances to RS may not have represented distinct microhabitat sites. Distances > 100 m were eliminated because distant sites may not have been available to the individual turtle at the time it selected its current position. Whether distance was measured upstream or downstream was determined by the toss of a coin.

At OS and RS, we simultaneously measured these variables: water temperature (TEMP) 5 cm above the bottom using a Type T thermocouple thermometer (TH-65, WesCor, Logan, UT) (0.1 °C), water depth (DPTH), distance from shore (DFS), distance to nearest standing tree (DFT) (0.01 m), submerged log size (LOGS), and log complexity (LOGC). LOGS and LOGC were measured by probing with a 3 m pole. Because we could not physically measure submerged logs, we classified LOGS and LOGC from 0 - 5. For LOGS, 0 corresponded to no logs at the site and 5 indicated the presence of large submerged logs. Likewise, a LOGC of 0 indicated 0 logs at the site, and 5 indicated presence of many different logs.

The paired approach inherent in the OS/RS method increased our power to detect differences between selected and available habitats over methods that compare unpaired means of habitat use and availability. Adequate sample size insured that the universe of potentially occupied microhabitats was included in the randomly chosen paired sites. In Results we report the distributions of OS and RS for each turtle subject and the pooled data. Each pair of OS/RS was independent among individuals. Alternative methods to test for temperature selection would have required measuring the temperature of the entire lake independently each time we examined an occupied microhabitat site. Use of the OS/RS method eliminated these pitfalls.

#### Thermoregulatory Patterns at Bingham Lake

Four subjects were fitted with an externally mounted temperature data logger (Stoway® Tidbit™, Onset Computer Corporation, Pocasset, MA) and a temperature data logger surgically implanted inside the body cavity 2 cm posterior to the plastron and anterior to the right hind limb. All procedures were carried out in accordance with an approved animal care protocol. The data loggers (weight = 14 g) recorded  $T_a$  and  $T_b$  every 24 minutes for 132 days ( $\pm 0.2$  °C). Turtles were released at the point of capture and then recaptured to retrieve recorded data. Two individuals were monitored from 2 August 1997 until 12 December 1997, 1 from 18 October 1997 until 27 February 1998, and for 1 individual from 12 June 1998 until 3 October 1998.

#### Habitat Selection Analyses at Bingham Lake

We used a paired t-test to test for differences in temperature between OS and RS. Unbalanced numbers of repeated measures among the telemetered individuals presented problems for paired analyses. We minimized lack of independence in the habitat

selection data set by analyzing means for each individual's OS/RS temperatures. This approach was statistically valid (Hurlbert 1984), but reduced our sample size from 158 observations of habitat use to 11 (the number of telemetered turtles for the habitat selection study). Moreover, averaging the data may mask some important variation. We used resampling statistics to evaluate the robustness of the habitat selection test (Hood 1999). The randomization routine reshuffled the OS and RS temperature data for each individual and recalculated the paired t-test. We obtained the frequency distribution of simulated t-values with a Monte Carlo analysis (5000 replicates), and calculated the probability that the critical t-value, ( $t_{0.05, 10} = 2.228$ ), was exceeded in the randomized tests. Low probability ( $<0.05$ ) of obtaining significant results in the randomized replicates would indicate the real test result was not spurious.

To determine the relationship between  $T_a$  and  $T_b$  of turtles in the field, we calculated linear regressions for each of the four turtles that were monitored with dataloggers, using  $T_a$  as the independent variable and  $T_b$  as the dependent variable, and compared the variances of  $T_a$  and  $T_b$  for each turtle with paired t-tests. We applied a square-root transformation to variances to correct skewness in the dataset. Once transformed, the values were unimodal and approximately normally distributed. To examine the extent and frequency that  $T_b$  differed from  $T_a$ , we subtracted  $T_a$  from  $T_b$  for the 4 paired time series, pooled. We calculated the frequency distribution of  $T_b - T_a$  differentials and tested for skewness and kurtosis to reveal patterns of differences between  $T_a$  and  $T_b$ . We examined daily patterns of  $T_b$  by computing and plotting pooled means for each of the 60, 24 minute, time periods each day.

We also calculated autocorrelation coefficients in the time series of  $T_b - T_a$  differentials to examine the extent to which differences between  $T_b$  and  $T_a$  were interdependent through time. If a subject remained at equilibrium with  $T_a$ , for example, differences between  $T_b$  and  $T_a$  would be close to zero through time and autocorrelation would be high. Autocorrelation values near zero would indicate the converse. A subject whose  $T_b$  was not in equilibrium with  $T_a$  should exhibit periods when differences between  $T_b$  and  $T_a$  were independent through time. This could occur in a subject moving through water of different temperatures, especially if long lag times were required for  $T_b$  to equilibrate with  $T_a$ .

Operative temperature ( $T_e$ , the integration of biophysical factors influencing  $T_b$ ) is the equilibrium temperature of an animal where it is currently positioned in the environment. Operative temperature can differ from other measures of environmental temperature, for example air temperature, because factors other than ambient temperature, (e.g., direct and indirect radiation), can influence the equilibrium  $T_b$ . The measurement of  $T_e$  presents problems for large ectotherms, particularly in the air, because of long time lags required for  $T_b$  to reach equilibrium. Measurement of equilibrium  $T_b$  and  $T_e$  of large animals in nature can be difficult in fluctuating environments because they may rarely reach equilibrium, and  $T_e$  is continually changing through time as environmental conditions change.

Problems measuring  $T_e$  are avoided for animals like *M. temminckii* that are entirely aquatic, remain in relatively deep (> 1 m), dark water, and never bask (Sloan and Taylor 1987, Ernst *et al.* 1994, Harrel *et al.* 1996). Factors other than temperature have low probability of affecting  $T_e$  because the high heat capacity of water results in very

rapid integration of all influences on water temperature. The water at our study site was stained and turbid, minimizing probability of solar and reflected radiation to directly influence  $T_b$ . There were no measurable currents in the lake, cold or hot springs, or any detectable temperature gradients at scales relevant to measurement of  $T_e$  for *M. temminckii* (e.g., vertical stratification 0.5 m off the bottom) that could create variability in water temperature at different points on the surface of even a large *M. temminckii*. Therefore we assumed the single temperature measured by the datalogger positioned on the carapace of the turtle adequately represented the temperature of the water surrounding the turtle. These characteristics of the study system coupled with fast rates of heat loss in water allowed us to assume  $T_e = T_b$ , and that turtles equilibrated to ambient water temperatures when stationary for several hours.

Differences between heating and cooling rates of turtles in the field were calculated, and heating and cooling time constants ( $\tau$ ) were calculated for each 24 minute interval for each turtle from the field. Tau (the time constant) is a mathematically derived constant equal to the time necessary for an organism's  $T_b$  to increase or decrease 63% of the difference between  $T_a$  and  $T_b$ . It is expressed in minutes and is independent of the magnitude of difference between  $T_a$  and  $T_b$ . Tau was calculated by regressing time on natural logs of differences between  $T_b$  and final temperature ( $\ln(T_b - T_f)$ ). The slope of the regression is  $-1/\tau$  (Bakken 1976, Neill and Stevens 1974, Turner 1987). We assumed study animals were not absorbing solar radiation and metabolic heat production was the mean difference between  $T_b$  and  $T_a$  for each turtle over the 132 day sampling period. The values of  $\tau$  for each 24-minute period were sorted according to whether the turtle was heating or cooling. We tested the null hypothesis that mean heating and cooling rates ( $\tau$ )

were equal using a paired *t*-test on differences between heating and cooling time constants from the field data.

To ascertain effects of size on cooling time constants, We subjected five *M. temminckii* to cooling trials in the laboratory. Subjects ranged in size from 0.7 kg to 26.25 kg. Turtles were maintained in the laboratory in metal tanks (115 cm X 60 cm) filled with water at 23 - 25°C for at least 2 weeks and fed fresh fish twice weekly. No food was offered for 2 days prior to each trial. Type T thermocouples were passed through a 16 Ga. hypodermic needle and inserted into the body cavity at the same location where miniature data loggers were implanted in subjects in the field. The thermocouple was held in place with a suture and attached to a CR10 data logger (Campbell Scientific, Logan, UT) programmed to measure and store temperature readings every 15 seconds. Water in the tanks was stirred with a small submersible pump to prevent thermal stratification. Ambient temperature was adjusted as needed by adding hot water or ice. We confirmed  $T_a$  varied  $<1.0$  °C by logging tank temperature at several places and inspecting temperatures after the trial. Trials consisted of placing the subject at room temperature into a tank at 32 °C. Once  $T_b$  reached 31.5 °C, We transferred the subject to a tank at 18 °C and logged  $T_b$  until it reached 18.5 °C. We then calculated cooling time constants from the resulting cooling curves.

## RESULTS

### Alligator Snapping Turtle Survey

A total of 1009 trap days were accomplished at 23 sites. Alligator Snapping Turtles were found at 17 of these sites. Site locations, trap days, and number of Alligator Snapping Turtles caught are presented in Table 1, sites are plotted on Map 1. These sites

sampled each of the major drainage systems from the Red River in the North to the Brazos River in the southwest. This area included the known historical range of the Alligator Snapping Turtle in Texas (Dixon 2000).

Our protocol had a very high likelihood of detecting Alligator Snapping Turtles when present. Traps were set for 3 consecutive nights at all sites, unless Alligator Snapping Turtles were detected early and the trip was concluded. The first Alligator Snapping Turtle was captured during the first trap night at 13 of the 17 sites (76.5% of cases), and during the first 2 nights at 15 of 17 sites (88.2% of cases). The first Alligator Snapping Turtle was caught on the third night only twice.

A total of 48 Alligator Snapping Turtles and an additional 471 individuals of 9 additional turtle species were captured (Table 2). Alligator snapping turtles were not caught at 6 sites: two from the Red – Sulphur River system in the northern portion of the study area, 2 sites on the Brazos – Navasota River system, Brazos Co. in the southwestern portion of the study area, at Ratcliff Lake in Houston Co. in the Neches River drainage, and Ayish Bayou in San Augustine Co.

Alligator Snapping Turtles were found at sites in all major drainages between the Sulphur River and the Navasota River. Twenty two additional records were obtained as a result of responses to the brochure/questionnaire and incidental records (Table 3).

These records (Collins et al. 2000, In Prep.) resulted in 8 new county records (Angelina, Jasper, Leon, Nacogdoches, San Jacinto, Collin, Sabine, and San Augustine) not previously recorded in a recent compilation of amphibian and reptile records for Texas (Dixon 2000). The county record from Collin County is an interesting locality because it is the most western record documented in Texas. We trapped a 46.4 kg

Alligator Snapping Turtle at a survey site in Collin Co., This locality lies in a northern reach of the Trinity River between Lake Ray Hubbard and Lake Lavon. Apparently, Alligator Snapping Turtles are persisting there at some level, despite extensive development in the region.

Map 2 details known county records for Texas from the literature and this study. Appendix 1 details the capture information and length and mass data for the Alligator Snapping Turtles trapped during the survey. Adult males had a maximum mid-line carapace length of 58.3 cm and a mass of 46.5 kg. Adult females had a maximum mid-line carapace length of 41.2 cm and a maximum mass of 16.8 kg. Adult males were generally larger (mean carapace length – 46.6 cm, mean mass – 25.3 kg) than adult females (mean carapace length – 41.2 cm, mean mass – 16.8 kg) (Table 4).

#### Habitat characteristics and habitat selection

Habitat measurements were compared between sites where Alligator Snapping Turtles were captured and sites where they were not captured (Table 5). Alligator Snapping Turtles were captured at sites that were characterized by significantly greater water depth at location of trap, greater water depth at deepest portion of channel, and greater percent cover of submerged vegetation than at trap sites where Alligator Snapping Turtles were not captured. All remaining habitat comparisons did not differ significantly between sites where turtles were and were not captured. The categorical habitat (type of structure, amount of structure, substrate type, bank profile, and species of nearest canopy tree) evaluations are presented in Figs. 1-5. Trap sites where Alligator Snapping Turtles were captured were more frequently characterized as having abundant structure compared to trap sites where Alligator Snapping Turtles were not captured (Fig1). The reverse was

found for sites having less abundant structure. No easily interpretable pattern was evident for structure type, bank profile, or substrate type (Figs. 2-4). This was most likely due to the baited traps drawing turtles into a variety of habitats. Nearest canopy tree included most of the common trees present, with a tendency for those species more tolerant of flooding to be better represented (Fig. 5).

#### Correlation between turtles trapped and evidence of trotline fishing

Trap sites, excluding those in the Red, Sulphur, Brazos, and Navasota drainages where no Alligator Snapping Turtles were captured, were also divided into two categories depending on the presence or absence of trotlines. No distinction was made between active and abandoned trotlines. Sites with trotlines present had fewer Alligator Snapping Turtle captures/trap day (15 turtles/347 trap days) compared to sites with trotlines absent (32 turtles/352 trap days). This difference was significant (Chi Square = 5.9,  $P = 0.015$ ). Mean median carapace lengths of adult Alligator Snapping Turtles at sites without trotlines (males 47.4 cm,  $n = 13$ ; females 42.1 cm,  $n = 12$ ) were greater than at sites with trotlines present (males 42.2 cm,  $n = 5$ ; females 39.9 cm,  $n = 9$ ). However, these differences were not significant for males ( $t = 1.269$ ,  $P = 0.117$ ) or females ( $t = 1.525$ ,  $P = 0.072$ ). Mean mass was also greater for both males and females where trotlines were absent (males 27.3 kg,  $n = 13$ ; females 18.3 kg,  $n = 12$ ) compared to sites where trotlines were present (males 18.4 kg,  $n = 5$ ; females 14.8 kg,  $n = 9$ ). These differences were significant for both males ( $t = 1.345$ ,  $P = 0.049$ ) and females ( $t = 2.177$ ,  $P = 0.043$ ).

#### The Turtle Population at Bingham Lake

Here, we report on captures of Alligator Snapping Turtles in Bingham Lake since May 1996. We caught 35 individual *M. temminckii* on 66 different occasions. The

capture per unit effort was 0.145 individuals per trap night. A trap night consisted of one trap set for one night. Individuals ranged in mass from 0.7 kg to 36.7 kg and 55.0 cm to 14.5 cm midline carapace length. The largest specimen was a male (55.0 cm midline carapace length, 36.7 kg), and the largest female measured 46.9 cm midline carapace length and 25.5 kg (Table 6). However, neither mean midline carapace length ( $T = 0.326$ ,  $df = 25$ ,  $p = 0.37$ ) nor mean mass ( $T = 0.417$ ,  $df = 25$ ,  $p = 0.34$ ) of males was significantly different from the mean length or mass of females. We trapped relatively few small individuals; most were greater than 26 cm (Figure 6). Only 11% were <26 cm straight-line carapace length and none <10 cm straight-line carapace length. Using mark/recapture data and NOREMARK software, we estimated the population was 43 individuals with 95% confidence limits of 38 - 56 individuals.

#### Movements and activity of Alligator Snapping Turtles in Bingham Lake

It was clear from both trapping and from telemetry data that all of the radiotagged individuals moved extensively throughout the lake. Radio tagged turtles moved daily during the warm seasons when we were in the field monitoring them. The branches of the Y-shaped Bingham Lake were most used by the telemetered turtles but they all used the rest of the lake as well. Additionally the turtles moved around the lake bottom both during the day and at night.

#### Habitat Selection

*Macrolemys temminckii* selected microhabitats based on structure. Means for individual turtles and pooled data are shown in Table 7. There were significant differences between OS and RS for LOGS ( $p < 0.05$ ) and LOGC ( $p < 0.05$ ), indicating turtles selected sites with larger logs and greater log complexity (Table 7). Turtles also

selected sites that were closer to shore than random sites; DFS and DFT both differed significantly ( $p < 0.05$ ) between OS and RS (Table 7). Surprisingly, DPTH was not different between OS and RS, despite the apparent preference for shoreline microhabitats. Surprisingly, DPTH was not different between OS and RS, despite the apparent preference for shoreline microhabitats.

*Macrolemys temminckii* occupied microhabitat sites that were warmer on average than randomly chosen non-sites. Mean microhabitat temperatures at 158 sites where turtles were found (mean = 19.25 °C) were significantly warmer than at paired RS locations (18.11 °C), and this difference was statistically significant ( $t = 2.91$ ,  $df = 10$ ,  $p = 0.015$ ) (Table 8). We used a randomization test to evaluate the robustness of this result (Hood 1999). The test randomized observed OS/RS data and recalculated the paired t-test (5000 replicates). The critical t-value, ( $t_{0.05, 10} = 2.228$ ), was never exceeded in the randomized test, yielding a very low probability ( $P < 0.0001$ ) the real test result was spurious. We also calculated a paired t-test on the pseudoreplicated data (all 158 observations pooled) and this result was also significant ( $t = 3.69$ ,  $df = 10$ ,  $p < 0.0004$ ).

Additionally, there was important variation in temperatures between OS and RS (Table 8). The mean of variances at RS (mean RS variance = 21.95°) was significantly greater than temperature variance at OS (mean OS variance = 15.41°) (paired t-test,  $t = -2.11$ ,  $df = 10$ ,  $p = 0.002$ ), indicating narrower range of temperature regimes at occupied microhabitat sites.

#### Seasonal and Daily Patterns of $T_b$ and $T_a$

Data loggers recorded  $T_a$  and  $T_b$  simultaneously from four turtles in the field, providing replicated measures of  $T_b - T_a$  differentials over long time series. The highest  $T_b$

experienced by any turtle was 32.62 °C while the lowest was 8.97 °C. Monthly mean  $T_b$  for the months sampled was highest in July (mean = 27.76 °C) and lowest in December (12.21 °C).

Body temperature was less extreme and more constant than  $T_a$  in all subjects. Mean monthly  $T_b$  closely matched mean monthly  $T_a$ , but  $T_a$  was more variable (Table 9). Daily patterns of  $T_b$  and  $T_a$  also showed strong correspondence, with greater fluctuations in daily  $T_a$  (Fig. 7). Maximum  $T_b$  was higher than maximum  $T_a$  and minimum  $T_a$  was lower than minimum  $T_b$  in every month (Table 9). Differences between minimum and maximum  $T_a$  and  $T_b$  were highest in summer months (July:  $T_b$  min -  $T_a$  min = 3.3 °C,  $T_a$  max -  $T_b$  max = 6.9 °C; August:  $T_b$  min -  $T_a$  min = 5.7 °C,  $T_a$  max -  $T_b$  max = 5.45 °C) and gradually decreased with onset of winter, with smallest differences between minimum and maximum  $T_a$  and  $T_b$  occurring in January (January:  $T_b$  min -  $T_a$  min = 0.38 °C,  $T_a$  max -  $T_b$  max = 0.27 °C).

There was a sine wave pattern of autocorrelation in sequential values of  $T_b - T_a$  differentials in all subjects. Autocorrelation decreased rapidly towards 0.00 over lags 1–5 (1 lag = 24 min temperature sampling), then increased and decreased with a wavelength of 60 time lags (one day) (Fig. 8). This diel cycle of differences between  $T_b$  and  $T_a$  could only be caused by a daily pattern of movements through different  $T_a$ s, for example deep or shallow water. Troughs in the autocorrelograms, when  $T_b - T_a$  differences were poorly correlated, corresponded to periods when turtles were moving, i.e., present  $T_b - T_a$  differences were independent of previous differences, or negatively correlated. Conversely, peaks corresponded to periods of relative inactivity, when  $T_b$  was more or less in equilibrium with  $T_a$ , and  $T_b - T_a$  differences were more correlated through time. The

pattern could not be caused by daily heating and cooling of microhabitat sites within the lake itself, because the lake changed temperature much more slowly than  $T_b$  for the largest *Macrolemys temminckii*. Stationary turtles'  $T_b$  would track the lake temperature and differences between  $T_b$  and  $T_a$  would remain close to zero and positively correlated through time. The amount of noise evident in the autocorrelograms (Fig. 8) was due to variation in  $T_a$  during the sampling periods. Turtle #21, for example, was monitored mostly in winter when  $T_a$  was relatively uniform throughout the lake. Autocorrelation in  $T_b-T_a$  differentials was either positive or zero for this subject, indicating that during winter there was probably less opportunity for large  $T_b-T_a$  differentials that would result in negative autocorrelation. Conversely, other subjects were monitored during warm months when  $T_a$  was more heterogeneous. Consequently autocorrelograms were noisier and larger  $T_b-T_a$  differentials produced periods of negative autocorrelation.

While there was a diel cycle of difference between  $T_b$  and  $T_a$ , there was no daily pattern of  $T_b$ . Monthly mean temperatures of the 60, 24 minute, periods of each day differed in most cases by less than 1 °C and never more than 2 °C (Fig. 9). Hence, turtles'  $T_b$  was relatively stable throughout the day, even though they were moving through waters of different temperatures.

### Thermoregulatory Patterns

*Macrolemys temminckii* were largely thermoconformers with  $T_b$  closely matching  $T_a$  (Fig. 10). Slopes of the regression lines formed by  $T_b$  and  $T_a$  for three turtles were very close to 1 (Slopes = 0.977, 0.992, 0.992) with  $R^2$  values ranging between 0.955 and 0.985. One subject (#30) differed from the rest in that its slope (0.837) and associated  $R^2$  (0.701) were slightly lower. There was more opportunity for variation

between  $T_b$  and  $T_a$  for this individual because it was monitored only in summer and early fall when  $T_a$  was more variable.

Differences between  $T_b$  and  $T_a$  for all turtles pooled were approximately normally distributed but clustered around the mean (kurtosis = 14.66) and slightly skewed to the left (skewness = -0.136) (Fig. 5). Mean  $T_b - T_a$  differentials equaled 0.32 °C. Minimum and maximum values were -9.33 °C and 7.62 °C, respectively, and 90 % of values fell between -0.84 °C and 1.24 °C indicating  $T_b$  was within 1.5 °C of  $T_a$  most of the time.

Body temperature increased rapidly when the subject was in a relatively warm environment and decreased slowly when the subject moved to a cooler site (Fig. 7).  $T_{aus}$  were also smaller when the *M. temminckii* were heating than when they were cooling (Table 10), and despite small sample size, the difference was significant (paired t,  $t = 3.18$ ,  $df = 3$ ,  $p < 0.02$ ). Additionally, variances in  $T_b$  were significantly smaller than variances in  $T_a$  (paired t,  $t = -6.82$ ,  $df = 4$ ,  $p = 0.016$ ) (Table 3).

#### Cooling Rates and Body Size

Cooling trials in the lab clearly showed larger *M. temminckii* cooled more slowly than smaller individuals (Table 11). The largest subject (26.25 kg) took 326 min to cool from 32 °C to 18 °C whereas the smallest individual (0.7 kg) cooled from 32 °C to 18 °C in 27.75 min. Log  $\tau$  and log mass scaled linearly [ $\log \tau = 0.803 \log \text{mass} - 1.52$  ( $r^2 = 0.947$ )] (Fig. 10).

#### Telemetry Study at Stephen F. Austin Experimental Forest

Five adult Alligator Snapping Turtles (4 females, 1 male) captured on the SFA Experimental Forest were instrumented with transmitters. The five turtles were tracked for 12 to 22 months between September 1999 and July 2001. One turtle has been

relocated and is still being monitored. The five turtles remained in a limited section of Bonaldo Creek, but made frequent movements within the segment (Maps 3-7). The length of stream segment used by the five turtles averaged 2.11 km (range 1.40 to 2.75). Turtles used both the permanent portion of the stream and the intermittent portion upstream. Upstream movement was presumably terminated by the box culvert passing under State Highway 7. Four individuals spent time in isolated pools during periods of low flow.

Habitat variables measured at turtle relocation points were compared with those of random points (Table 12). Turtle relocation points were characterized by significantly greater water depth, maximum water depth within 5 m, stream width and distance to shore (Table 12). All of these measures indicate that Alligator Snapping Turtles were using the larger pools of the stream available. Alligator Snapping Turtle locations were also characterized by larger diameter of nearest log (Table 12). Significant relationships were not found for the other quantified habitat variables reported in Table 12.

Figures 12-15 illustrate the patterns of categorical habitat variables (amount of structure, type of structure, substrate type and nearest canopy tree). Alligator Snapping Turtles were associated with sites having more structure (Fig. 12). This was primarily due to a strong association of Alligator Snapping Turtles with submerged logs (Fig. 13). The relationship with substrate type was also clear. Alligator Snapping Turtles were found preferentially in sites with leaf and detritus substrates (Fig. 14). This was presumably due to the frequent use of deeper pools where such organic materials tended to accumulate. No clear patterns are evident in relation to the nearest canopy tree (Fig. 15).

## DISCUSSION

### Distribution of *Macrolemys temminckii* in Texas

Trapping surveys revealed that Alligator Snapping Turtles are still widely distributed within their historic range in Texas, and our surveys provided 8 new county records for *Macrolemys temminckii* in Texas. We did not find Alligator Snapping Turtles at our trapping sites in the Red/Sulphur drainage, but historical records are known from this drainage and we know of anecdotal reports of Alligator Snapping Turtles from the area. A professional ecologist and her students observed a dead Alligator Snapping Turtle left on a log in the Sulphur River in 1999 (Dr. F. Gelwick, Texas A&M, pers. comm.). We did not document Alligator Snapping Turtles in the Brazos or Navasota Rivers despite 6 nights of trapping. It is therefore doubtful that Alligator Snapping Turtles occur west of the Trinity River drainage, and our surveys appear to delimit the western range of the species in Texas.

Several historical localities for Alligator Snapping Turtles in Texas merit commentary. In the Catalogue of American Amphibians and Reptiles species account for *Macrolemys temminckii*, Lovich (1993) included historical localities in the San Antonio River and Colorado River drainages. These records are extremely doubtful. In his monograph, Pritchard (1989) discounted these records and quoted J. Dobie's letter to him, "I do not remember where I found the *Macrolemys* records for the San Antonio and Colorado Rivers. I feel sure they do not occur in either." Pritchard goes on to report the Colorado River record was probably based on Agassiz (1857) who quoted a resident of Austin who claimed *Macrolemys* was not rare around Austin, but not as large as specimens from Mississippi.

We obtained an unmistakable photograph taken by Dr. Delbert Gatlin, Texas A&M University, of an adult *Macrolemys temminckii* found at the Aquatic Research and Teaching Facility on the floodplain of the Brazos River near the crossing of Hwy. 60 in Brazos County. This record is unusual because it is outside the known range of the species, and would represent a significant westward extension of the range into the Brazos River drainage. Interestingly, however, fossils of *Macrolemys* sp. are known from deposits of the Brazos River from Late Pleistocene to Recent (Lovich 1993). The specimen was found on land away from the river by staff working at the aquaculture center, that is adjacent to Highway 60. The circumstances of the observation leave serious doubt whether the individual was naturally occurring, or could have been a released captive. Extensive conversations with herpetologists familiar with the range and habitat requirements of *Macrolemys temminckii* lead us to doubt this record. Therefore, we do not consider the photograph of the individual from the Brazos River a verifiable naturally occurring locality for *Macrolemys temminckii*. Additionally, we trapped for 3 nights in the Brazos River in suitable habitat near this location, and for 3 nights in the Navasota River, and did not detect Alligator Snapping Turtles.

Summarizing, we found Alligator Snapping Turtles throughout their known historical range in Texas, including several new localities. We found no evidence of range contraction, and documented the species in 8 counties where it was not found previously. Our study helped define the geographic distribution of the species in Texas at the scale of major reaches of the river drainages, but of course we did not document the fine-scaled distribution of the species in all of the potential habitat sites within its range.

Movements and activity

Alligator Snapping Turtles move extensively. Previous telemetry studies have documented movements of up to 6.8 km and home ranges of over 200 ha (Sloan and Taylor 1987). The turtles in Bingham Lake used the entire area of the 3.4 km long oxbow lake. The situation in Bonaldo Creek was substantially different. Although the linear extent of home ranges averaged 2.1 km in length, the actual home range area was limited to less than 5 ha due to the limited width of the creek channel. Despite this limitation, a minimum of 5 adult Alligator Snapping Turtles occupied an approximately 4 km segment of stream with substantial overlap in home ranges.

#### The Habitat of *Macrolemys temminckii*

##### Habitat complexity

The results from the distribution surveys, habitat selection studies at Bingham Lake, observations of telemetered turtles at Bonaldo Creek, and published literature all converge on the conclusion that Alligator Snapping Turtles use complex underwater microhabitat sites such as submerged logs, undercut banks, or other features that create cover. In our study, *Macrolemys temminckii* clearly selected microhabitats containing both large logs and complex arrangements of logs. Because they selected sites with logs, we suspect they were also predisposed to select sites closer to the shore and closer to trees. Logs were usually found closer to the bank and the nearest tree was always along the shore. By selecting sites containing logs, *M. temminckii* also selected sites closer to the shore and standing trees.

Although we demonstrated *M. temminckii* preferred complex microhabitats, this study did not elucidate mechanisms driving selection of sites containing logs. Possible

explanations include selection for cover to avoid predation, or preference for cover to aid foraging in this ambush predator. Werner and Hall (1988) presented evidence that bluegills (*Lepomis macrochirus*) used dense cover to avoid predators, but adult *M. temminckii* have no known predators (Pritchard 1989). A better explanation might be logs were used to avoid conspecifics. Agonistic behaviors were documented for both male/male and male/female encounters (Ernst *et al.* 1994), and it is possible turtles seek refuge to avoid intraspecific interactions.

Harrel *et al.* (1996) suggested *M. temminckii*'s preference for dense cover may be a foraging strategy advantageous for an ambush predator. Complex or dense cover could serve as camouflage, or complex habitat patches may contain high densities of prey. We did not measure prey density during this study, but it is reasonable that sites containing logs could be areas of concentrations of centrarchid fishes living in the habitats.

Alligator Snapping Turtles are sit-and-wait predators and possess a lingual appendage (Spindel *et al.* 1987) used to lure fish into the mouth (Allen and Neill 1950). However, use of the lingual lure is a trait ascribed primarily to juveniles (Pritchard 1989); and most *M. temminckii* observed in this study were adults. *Macrolemys temminckii* are known to prey on smaller turtles (Ernst *et al.* 1994) and sites with logs often served as basking areas for other turtle species in the area. None of these behavioral mechanisms are mutually exclusive, and we suggest *M. temminckii* probably was selecting complex microhabitat sites for resting, foraging, and refuge.

#### Temperature selection

*Macrolemys temminckii*  $T_{bs}$  generally conformed to environmental temperatures in the field. Turtles that were warmer or cooler than their surroundings eventually

equilibrated to ambient temperature presumably because of high rates of heat exchange in the aquatic medium. Although  $T_b$  rarely differed from  $T_a$  by more than 1.5 °C, there were periods when differences between  $T_b$  and  $T_a$  were great, leaving the potential for some control of  $T_b$  through behavioral and physiological mechanisms.

Shine and Madsen (1996) suggested thermoregulatory behaviors may be unimportant to large reptiles. They found water pythons (*Liasis fuscus*) maintained stable  $T_b$  without overt thermoregulatory behavior and found no evidence of temperature-based microhabitat selection. They attributed lack of thermoregulation in this species to abundance of suitable  $T_a$ s and thermal inertia. For *M. temminckii*, not all microhabitats were thermally equivalent. We showed *M. temminckii* did select relatively warmer microhabitat sites based on their availability in the environment and occupied sites that were less variable in temperature than random non-sites. Hence, the turtles selected a surprisingly narrow range of microhabitats that were relatively warm. Large saltwater crocodiles (*Crocodylus porosus*) controlled  $T_b$  via basking and shuttling between warm and cool microhabitats (Seebacher *et al.* 1999). Unlike crocodylians, however, *M. temminckii* do not bask and we suggest temperature selection was probably the only mechanism whereby *M. temminckii* could exert control of  $T_b$  for long periods when  $T_b$  would eventually reach equilibrium with  $T_a$ . Selection of microhabitats based on temperature was apparent for *M. temminckii*, and we suggest it was important to their thermoregulation.

Daily average  $T_b$  during each month was surprisingly stable (Figure 3) and  $T_b$  was tightly correlated with  $T_a$  (Figure 4). These results occurred because *M. temminckii* remaining in one spot equilibrated to  $T_a$ . However, the distribution of  $T_b$ - $T_a$  differentials

showed  $T_b$  was different from  $T_a$  in many cases. Autocorrelation analysis revealed a diel pattern in the temporal correlation of these differences. We interpreted periodicity in autocorrelation of  $T_b-T_a$  differentials reflected a circadian activity pattern of these turtles moving into cooler or warmer water. Turtles move for many reasons, and we do not suggest movements were principally for thermoregulatory reasons. The result is interesting, however, because periods of low or negative autocorrelation between  $T_b-T_a$  differences reflected periods when differences in  $T_b-T_a$  were mediated by thermal inertia and physiological controls.

Our results suggest *M. temminckii* exhibited some physiological control over body temperatures. Turtles in the field had smaller heating time constants than cooling time constants. *Macrochelys temminckii* heated more rapidly than they cooled presumably because of physiological phenomena such as changes in heart rate, blood shunting, and blood flow to extremities that are well known in turtles and other large reptiles (Weathers and White 1971, Pough *et al.* 1998).

In addition to the physiological controls *M. temminckii* presumably exerted over rates of heat loss, we confirmed thermal inertia in *M. temminckii* and described the relationship between cooling rate and body size. The effect of thermal inertia coupled with physiological control over rates of heat loss resulted in less extreme and less variable values of  $T_b$  than  $T_a$ . Thermal inertia and physiology apparently created the potential for *M. temminckii* to extend the range of habitats exploited and the amount of time spent there before reaching equilibrium with  $T_a$ .

Because of their life history characteristics, population growth is expected to be very sensitive to adult survivorship (Congdon *et al.* 1993). Hence, populations of

Alligator Snapping Turtles can be severely impacted by removal of adults, and population recovery would be slow without immigration. The species is easily trapped and exploitation can rapidly impact numbers of mature adults (Congdon et al. 1993; Sloan and Lovich 1995; Wagner et al. 1996). Past commercial harvest in Arkansas has resulted in population level changes evident even after commercial harvest ceased (Wagner et al. 1996). The continuing commercial harvest in Louisiana has caused concern (Sloan and Lovich 1995) and potentially could impact populations in adjacent states through illegal harvest.

The species is protected in Texas, however the level of illegal and incidental take is unknown. Results from this survey suggest that incidental take on trotlines may be substantial enough to impact populations. Our limited data are not sufficient to estimate levels of capture on trotlines or the ultimate fate of individuals caught on trotlines.

#### Recommendations and Future Research

Future research on distribution of *Macrochelys temminckii* in Texas could be aimed at determining the presence and absence of the species throughout the individual river drainages where it is known to occur. It may also be important to document the presence or absence of Alligator Snapping Turtles in reservoirs within its range.

Of particular importance is documenting the impact of incidental take of Alligator Snapping Turtles by fisherpersons, especially those using trotlines. Our results that trapping success was lower and turtle sizes were possibly lower at sites with trotlines should be taken as a warning sign that Alligator Snapping Turtle populations in areas that are heavily fished may be impacted. In Texas, incidental take is probably more important than hunting Alligator Snapping Turtles per se, and efforts to educate the public to

release Alligator Snapping Turtles unharmed may be worthwhile. Additional research on the impact of incidental take, especially through the use of trotlines is a high priority.

The results that habitat complexity is important to Alligator Snapping Turtles and that they actively select microhabitat sites based on structure and temperature have meaningful implications for conservation. Alligator Snapping Turtles need appropriate sites for foraging and cover, and it is unknown how populations may persist in areas where underwater habitat complexity has been reduced.

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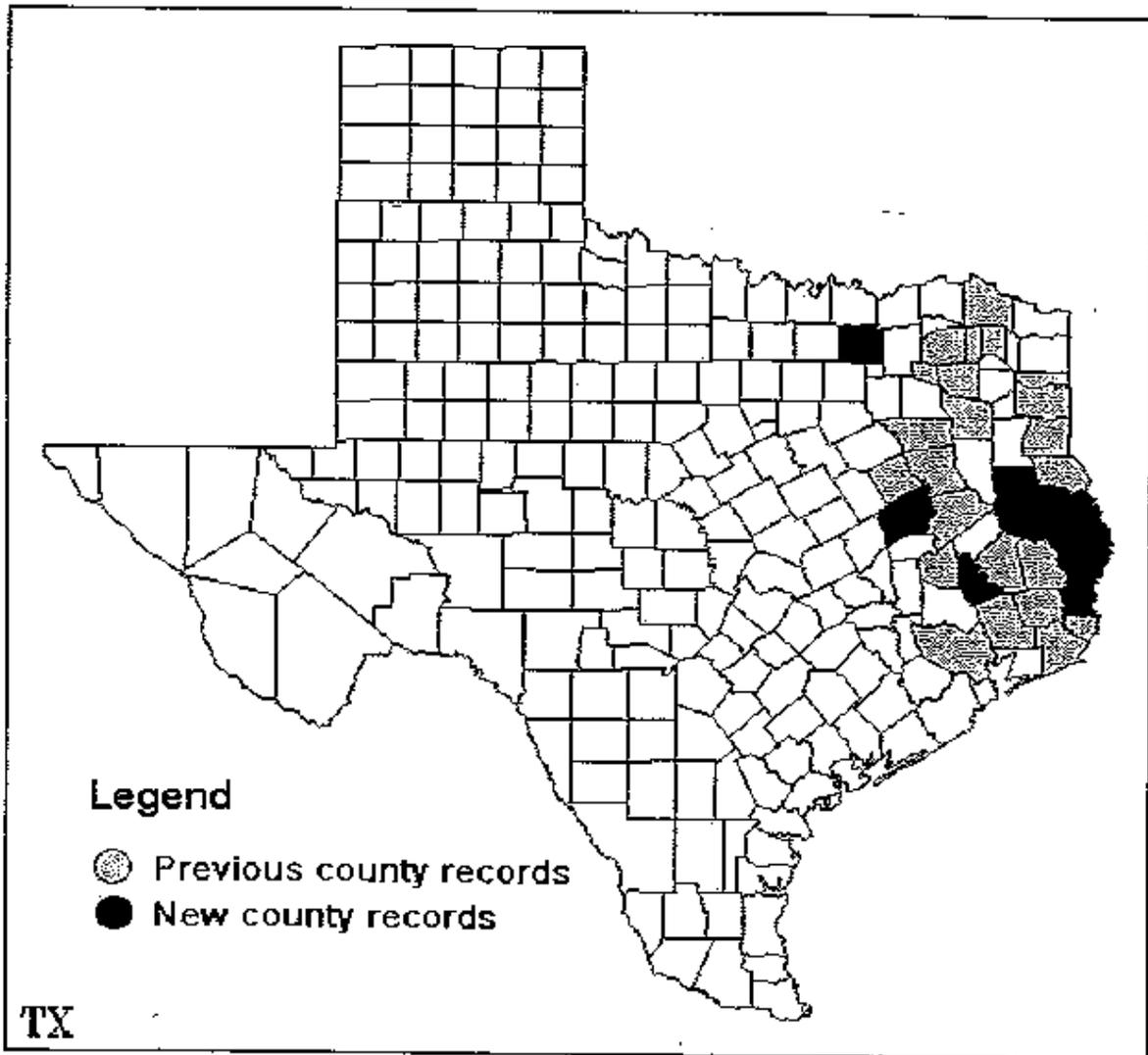
## LITERATURE CITED

- ALLEN, R. R. AND W. T. NEILL. 1950. The Alligator Snapping Turtle, (*Macroclemys temminckii*), in Florida. Spec. Publ. Number 4, Ross Allen's Reptile Institute, Silver Springs, Florida.
- BAKKEN, G.S. 1976. An improved method for determining thermal conductance and equilibrium body temperature with cooling curve experiments. *Journal of Thermal Biology* 1: 169-175.
- Collins, C. S., D. Saenz, and J. R. McCormick. 2000. *Macroclemys temminckii* (Alligator Snapping Turtle). *Herp. Rev.*
- Conant, R., and J. T. Collins. 1991. A field guide to the reptiles and amphibians of eastern and central North America. Houghton Mifflin Co., New York, New York.
- Congdon, J. D., A. E. Dunham, and R. C. van Loven Sels. 1994. Demographics of common snapping turtle (*Chelydra serpentina*): implications for conservation management of long-lived organisms. *Amer. Zool.* 34:397-408.
- Dixon, J. R. 2000. Amphibians and reptiles of Texas. Texas A&M University Press. College Station, Texas.
- Dobie, J. L. 1971. Reproduction and growth in the alligator snapping turtle, *Macroclemys temminckii*. *Copeia* 1971:645-658.
- ERNST, C.H., J.E. LOVICH, AND R.W. BARBOUR. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington D.C.
- HARREL, J.B., C.M. ALLEN, AND S.J. HERBERT. 1996. Movements and habitat use of subadult alligator snapping turtles (*Macroclemys temminckii*) in Louisiana. *American Midland Naturalist* 135: 60-67.

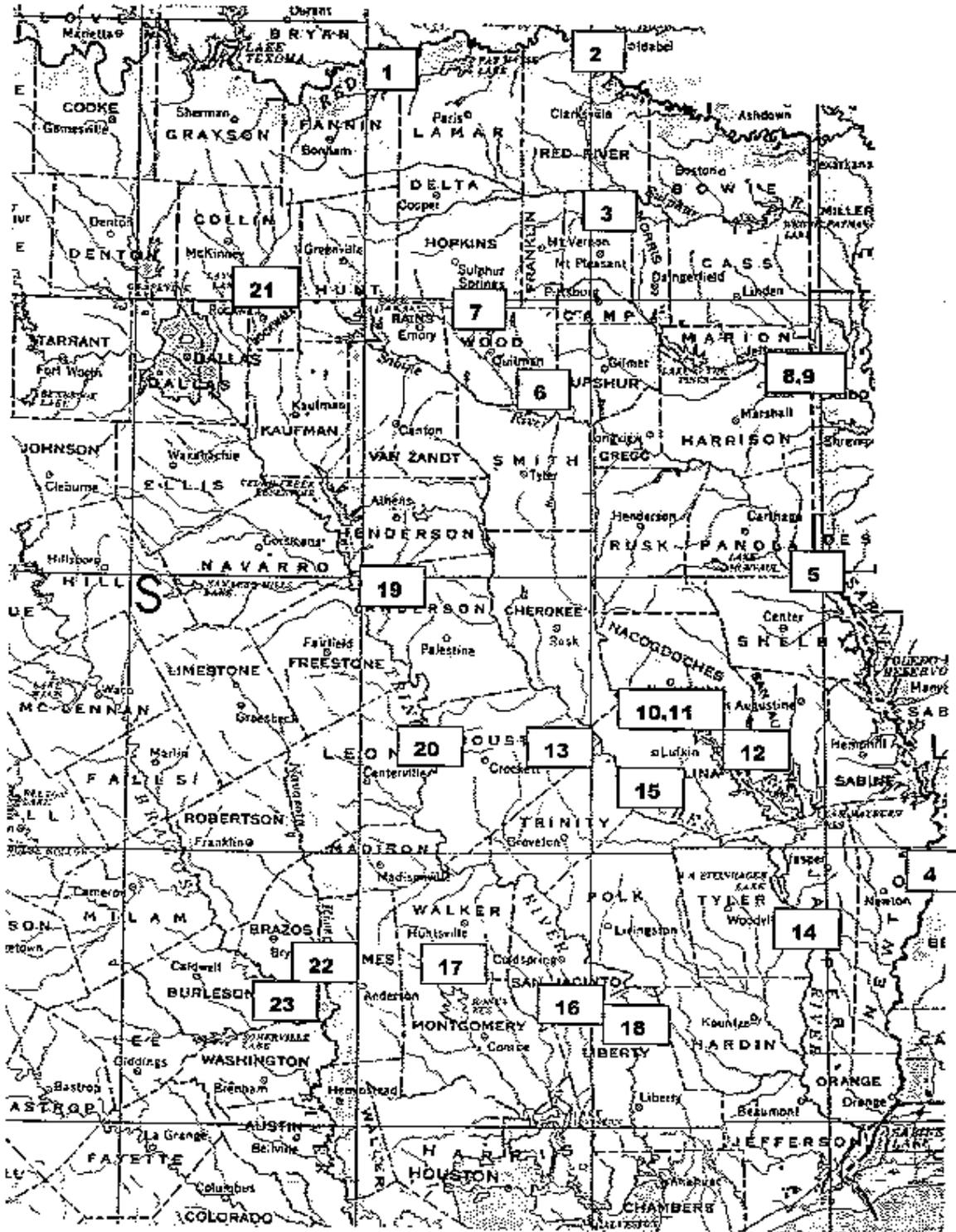
- Lovich, J.E. 1993. *Macroclmys, M. temminckii*. Catalogue of American Amphibians and Reptiles. 562.1-562.4.
- NEILL, W.H., AND E.D. STEVENS. 1974. Thermal inertia versus thermoregulation in "warm" turtles and tunas. *Science* 184: 1008-1010.
- Pritchard, P. C. H. 1989. The alligator snapping turtle: biology and conservation. Milwaukee Public Mus., Milwaukee, WI.
- POUGH, F.H., R.M. ANDREWS, J.E. CADLE, M.L. CRUMP, A.H. SAVITZKY, AND K.D. WELLS. 1998. Herpetology. Prentice Hall, New Jersey.
- Roman, J., S. D. Santhuff, P. E. Moleer, and B. W. Bowen. 1999. Population structure and cryptic evolutionary units in the alligator snapping turtle. *Cons. Biol.* 13:135-142.
- SEEBACHER, F., G.C. GRIGG, AND L.A. BEARD. 1999. Crocodiles as dinosaurs: Behavioral thermoregulation in very large ectotherms leads to large and stable body temperatures. *The Journal of Experimental Biology* 202: 77-86.
- SHINE, R., AND T. MADSEN. 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiological Zoology* 69, 252-269.
- SLOAN, K.N., AND D. TAYLOR. 1987. Habitats and movements of the alligator snapping turtle in Louisiana. *Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies* 41: 343-348.
- Spindel, E. L., J. L. Dobie, and D. F. Buston. 1987. Functional mechanisms and histological composition of the lingual appendage in the alligator snapping turtle, *Macroclmys temminckii*. *J. Morphology* 194:287-301.

- TURNER, J.S. 1987. The cardiovascular control of heat exchange: consequences of body size. *American Zoologist* 27: 69-79.
- Wagner, B. K., D. Urbston, and D. Leek. 1996. Status and distribution of the alligator snapping turtle in Arkansas. *Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies* 50:264-270.
- WEATHERS, W.W., AND F.N. WHITE. 1971. Physiological thermoregulation in turtles. *American Journal of Physiology* 221: 704-710.

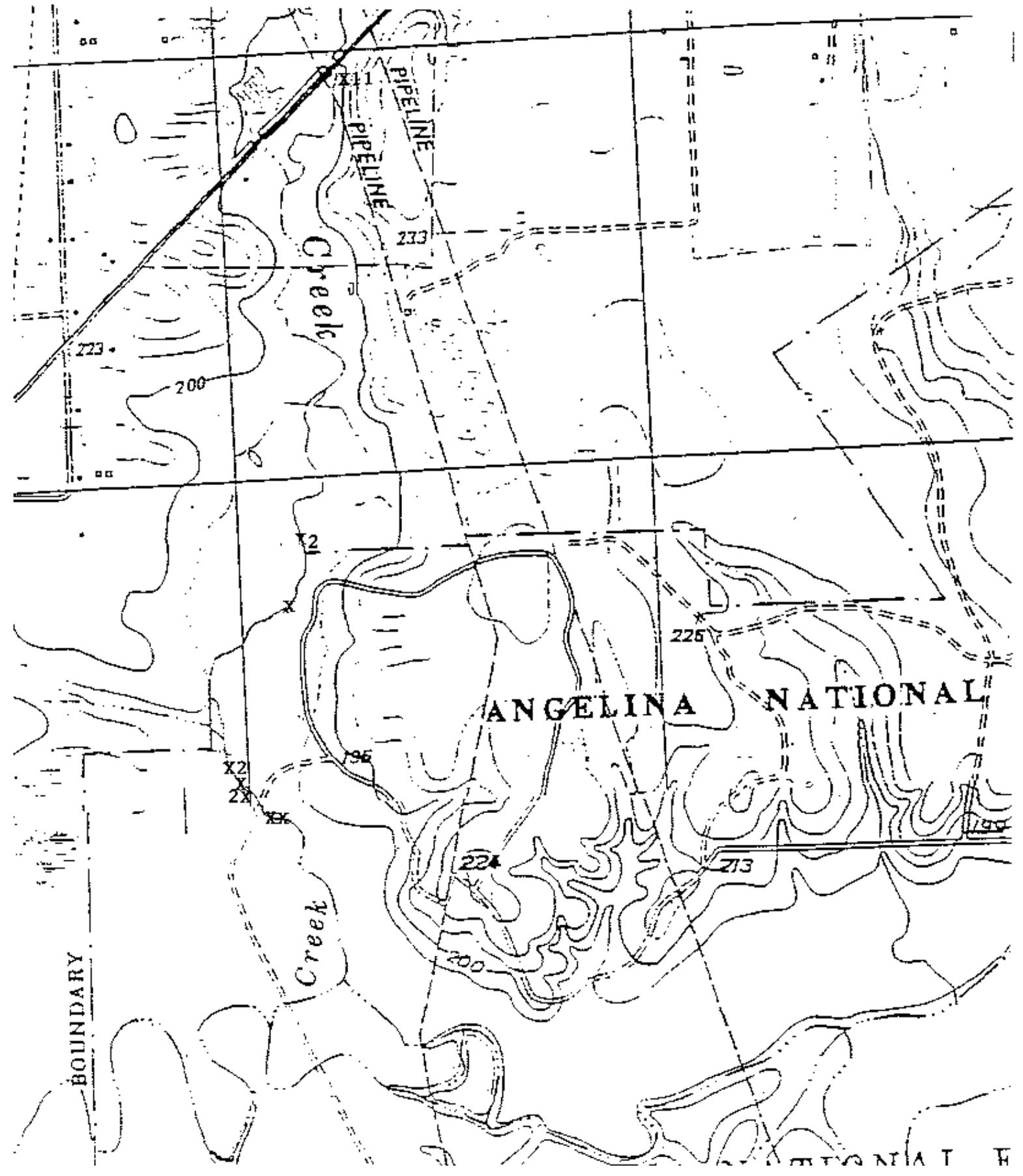
**Map 1. County records for Alligator Snapping Turtles in Texas**



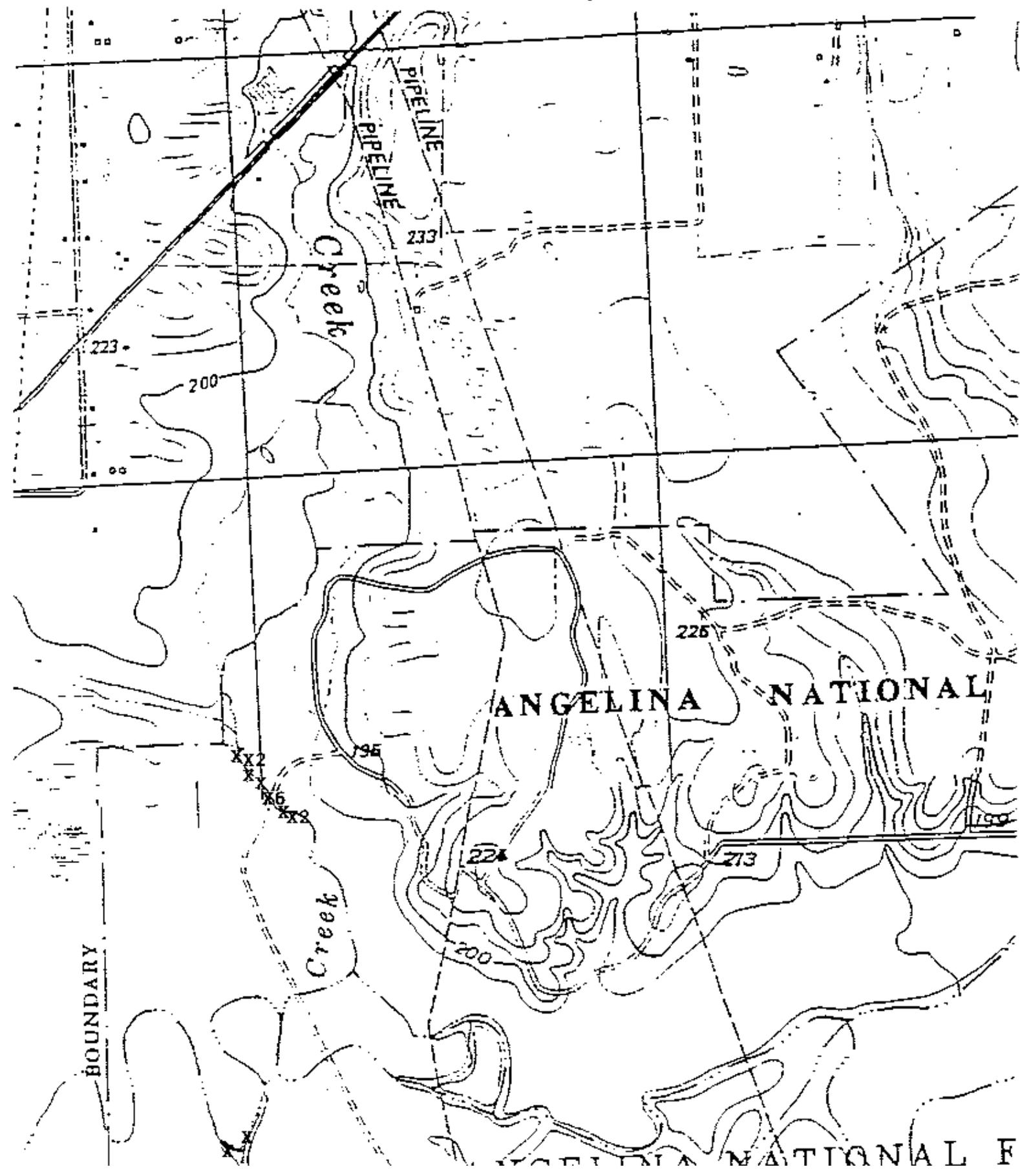
**Map 2. Alligator Snapping Turtle survey localities in Texas, 1999-2001.**



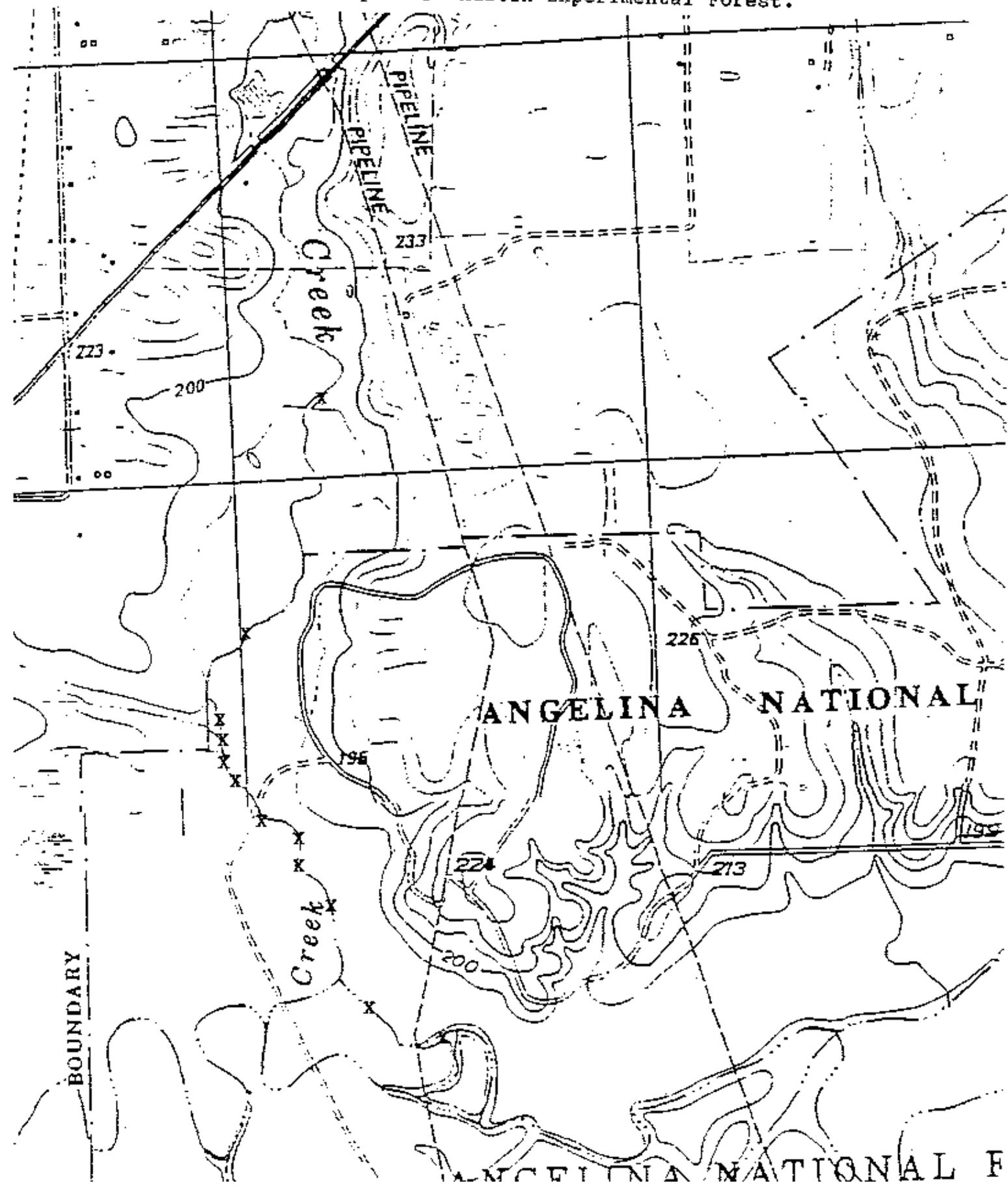
Map 3. Radiotelemetry locations of Alligator Snapping Turtle #173 at Stephen F. Austin Experimental Forest.



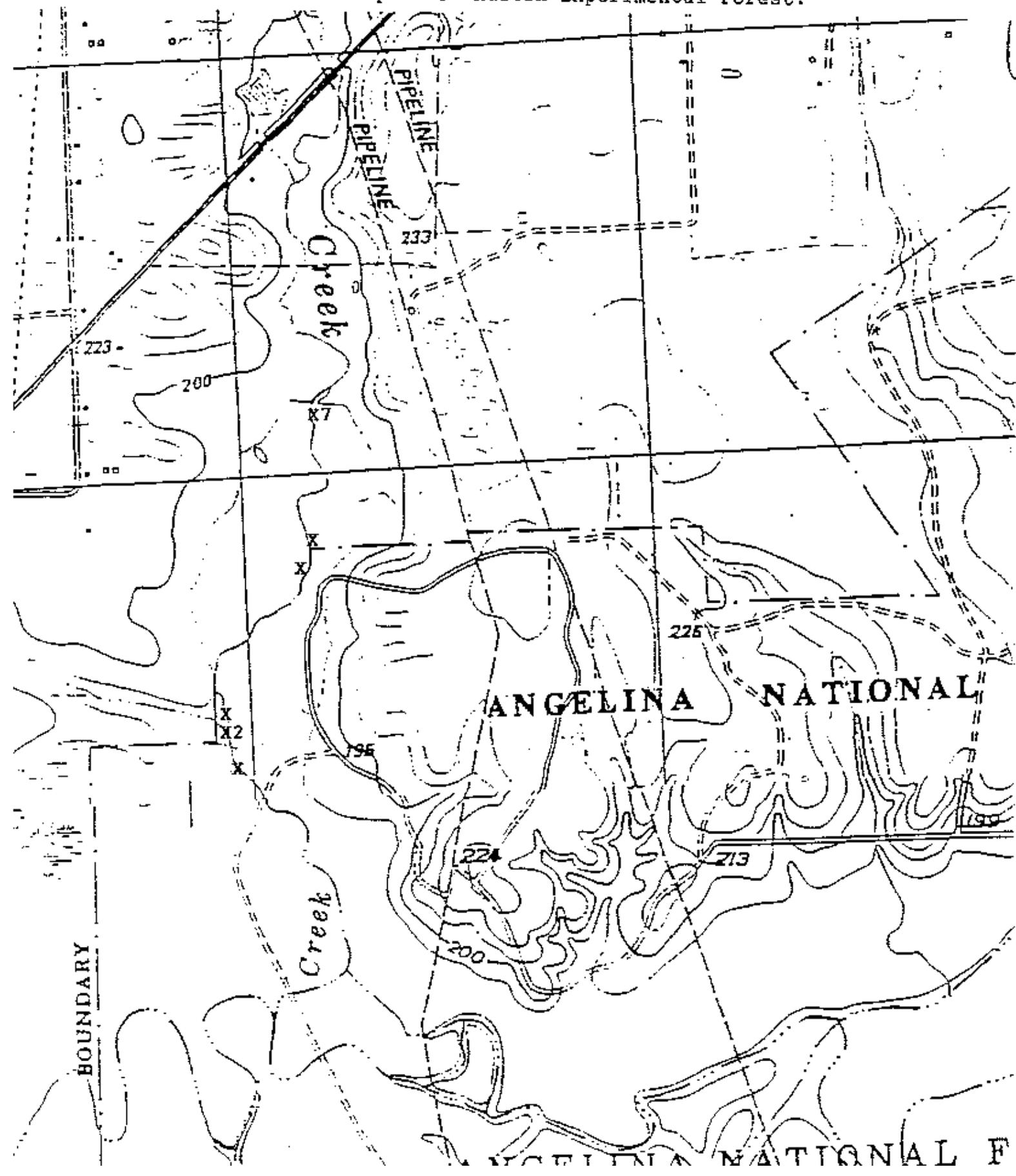
Map 4. Radio-telemetry locations of Alligator Snapping Turtle #153 at Stephen F. Austin Experimental Forest.



Map 5. Radio-telemetry locations of Alligator Snapping Turtle #294 at Stephen F. Austin Experimental Forest.



Map 6. Radio-telemetry locations of Alligator Snapping Turtle #233 at Stephen F. Austin Experimental Forest.



Map 7. Radio-telemetry locations of Alligator Snapping Turtle #254 at Stephen F. Austin Experimental Forest.

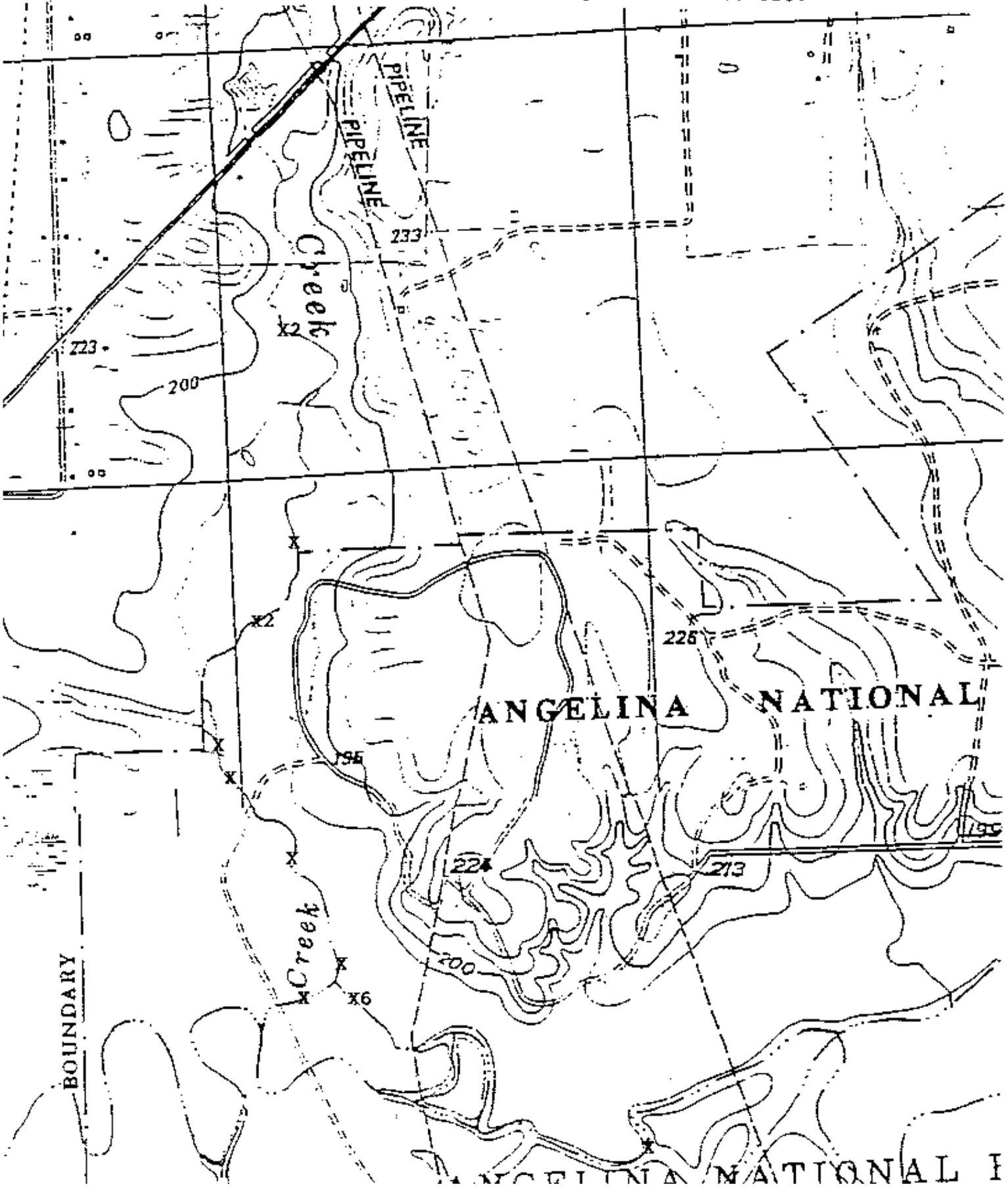


Table 1. Alligator snapping turtle trap locations.

DRAINAGE	COUNTY	LOCATION	DATE	TRAP DAYS
Red River	Fannin	Bois D'Arc Creek	9-11 April 2001	45
Red River	Red River	Greenwood Branch	21-23 June 2000	40
Sulphur River	Titus	White Oak Creek	23-25 May 2001	45
Sabine River	Newton	Lost Creek; Big Cow Creek	19-21 Oct. 2000	47
Sabine River	Shelby	Swede Johnson Lake	17-19 Aug. 2000	45
Sabine River	Wood	Beaver Lake	20-22 July 1999	45
Sabine River	Wood	Lake Fork at Running Creek	13-15 June 2001	45
Cypress River	Harrison	Caddo Lake	12-14 May 2000	15
Cypress River	Harrison	Harrison Bayou	12-14 May 2000	30
Angelina River	Angelina	Angelina River	25-27 May 1999	30
Angelina River	Angelina	Bonaldo Creek	various	55
Angelina River	San Augustine	Ayish Bayou	13-15 July 2001	45
Neches River	Houston	Ratcliff Lake	19-21 Aug. 2001	45
Neches River	Tyler	Bingham Lake	24-25 Aug. 2000	72
Neches River	Angelina	Old Neches Lake	15-17 May 2001	45
San Jacinto River	San Jacinto	East Fork	27-29 Sept. 2000	45
San Jacinto River	San Jacinto	West Fork	16-18 June 2001	45
Trinity River	Liberty	Pickett's Bayou	25-27 July 2000	45
Trinity River	Anderson	Catfish Creek, Engling WMA	8-10 June 1999	45
Trinity River	Leon	Keechi Creek WMA	14-16 July 1999	45
Trinity River	Collin	Trinity River	15-17 Aug. 2001	45
Navasota River	Brazos/Grimes	Navasota River	16-18 June 1999	45
Brazos River	Brazos/Burleson	Brazos River	21-23 June 2000	45

Table 2. Turtle captures during surveys for alligator snapping turtles (*Macrolemys temminckii*).

DRAINAGE	SITE	<i>M. temminckii</i>	<i>C. serpentina</i>	<i>S. odoratus</i>	<i>S. carinatus</i>	<i>K. subrubrum</i>	<i>G. kohnii</i>	<i>G. pseudo-geographica</i>	<i>T. scripta</i>	<i>P. concinna</i>	<i>A. spinifera</i>
Red River	Bois D'arc Creek	0	0	0	0	0	2	0	5	2	28
	Greenwood Branch	0	18	6	0	0	0	0	108	0	1
Sulphur River	White Oak Creek	0	0	0	15	0	2	0	9	0	3
Sabine River	Lost Creek	2	0	0	18	0	0	0	22	0	0
	Swede Johnson Bayou	4	0	0	1	0	0	0	16	1	0
	Beaver Lake	4	0	0	0	0	2	0	12	1	2
	Lake Fork	2	2	0	0	0	0	0	55	0	1
Cypress River	Caddo Lake	4	0	0	0	0	0	0	4	0	0
	Harrison Bayou	3	0	0	0	0	0	0	6	0	0
Angelina River	Angelina River	1	0	0	0	0	0	1	1	0	0
	Bonaldo Creek	5	6	0	0	0	0	0	0	0	0
	Ayish Bayou	0	0	0	0	0	0	0	1	0	0
Neches River	Ratcliff Lake	0	0	2	0	1	0	0	11	0	0
	Bingham Lake	2	0	0	2	0	0	0	5	0	0
	Old Neches	5	0	0	6	0	1	0	15	0	6

Table 2. Turtle captures during surveys for alligator snapping turtles (*Macrolemys temminckii*).

San Jacinto River	East Fork	1	0	0	3	0	0	0	3	0	0
	West Fork	2	3	0	23	0	0	0	1	0	1
Trinity River	Pickett's Bayou	1	0	0	0	0	0	0	0	0	2
	Catfish Creek	3	0	0	1	0	0	0	1	0	0
	Keechi Creek	8	0	0	0	0	0	0	2	0	7
	Collin County	1	1	0	0	0	0	0	19	0	1
Navasota River	Navasota River	0	6	0	1	0	13	0	11	0	4
Brazos River	Brazos River	0	0	0	0	0	4	0	33	0	9
<b>TOTALS</b>	<b>23 Sites</b>	<b>48</b>	<b>36</b>	<b>8</b>	<b>81</b>	<b>1</b>	<b>22</b>	<b>1</b>	<b>250</b>	<b>4</b>	<b>65</b>

Table 3. Miscellaneous alligator snapping turtle records.

DRAINAGE	COUNTY	LOCATION	DATE	SEX	LENGTH	MASS	COMMENTS	OBSERVER
Sabine	Panola	Sabine River					Trotline (live)	Tom Gallenbach
Sabine	Panola	Sabine river					Trotline (dead)	Tom Gallenbach
Sabine	Wood	Quitman Reservoir	May 1998				Trotline (live)	Ronny Ward
Sabine	Wood	Lake Fork Reservoir	May 1996				Trotline (live)	Ronny Ward
Sabine	Sabine	Toledo Bend Reservoir	Sept. 2000		2 ft.		Alive while fishing	Hulett Evans
Sabine	Sabine	Toledo Bend Reservoir	Sept. 2000		3 ft		Alive while fishing	Hulett Evans
Sabine	Panola	Lake Murvaul	2 June 2001		30 inches		Trotline (live)	Our records
Sabine	Orange	Pine Island Bayou					Trotline (dead)	Law Enforcement Officer
Sabine	Shelby	Toledo Bend Reservoir	1 Dec. 2000	male	61.9 cm	43 kg	Dead	Our records
Sabine	Shelby	Prairie Creek	8 May 2000	female	35.2 cm	9.5 kg		Our records
Angelina	Nacogdoches	Nacogdoches	10 May 2001	male	52.2 cm	33.8 kg		Our records
Angelina	Nacogdoches	Lake Nacogdoches	1984		34 cm		Dead (gunshot)	Our records
Angelina	Jasper	Sam Rayburn Reservoir	Nov. 2001	female	38.1 cm	14.2 kg	Caught on hook and line	Gene Hemphill
Neches	Henderson	Lake	Spring				Trotline	Rob Seaver

Table 3. Miscellaneous alligator snapping turtle records.

		Palentine	2000				(dead)	
Neches	Hardin	Village Creek					Alive	Game Warden
Trinity	Van Zandt	Cedar Creek			64.7 cm	42.5 kg	Alive (photo)	Steven Stapleton
Trinity	Anderson	Catfish Creek			27 inches		Trotline (live) (photo)	Curtis Munsinger
Trinity	Liberty		June 1998			70 lbs.	Nuisance turtle call	Gary Cain

**Table 4. Size (length and mass) of Alligator Snapping Turtles captured in Texas during 1999-2001.**

	<b>MALE n = (19)</b>	<b>FEMALE (n = 21)</b>	<b>JUVENILE (n = 8)</b>	<b>TOTAL (n = 48)</b>
<b>MINIMUM CARAPACE LENGTH (CM)</b>	30.4	35.1	15.5	
<b>MAXIMUM CARAPACE LENGTH</b>	58.3	46.1	29.0	
<b>MEAN CARAPACE LENGTH (CM)</b>	46.6	41.2	25.1	40.6
<b>MINIMUM MASS (KG)</b>	6.8	10.2	0.8	
<b>MAXIMUM MASS (KG)</b>	46.5	23.8	6.0	
<b>MEAN MASS (KG)</b>	25.3	16.8	4.1	18.3

Table 5. Comparison of habitat variables at traps that captured Alligator Snapping Turtles (n = 48) and at traps that were unsuccessful (n = 239).

HABITAT VARIABLE	TURTLE CAPTURE POINTS (MEAN, SD)	RANDOM POINTS (MEAN, SD)	P
Depth at Trap (m)	1.35 (0.41)	1.54 (0.65)	0.035
Channel Depth (m)	1.75 (0.70)	2.20 (1.10)	0.008
Stream Width (m)	33.6 (44.13)	32.6 (33.82)	0.900
Distance to Shore (m)	6.0 (7.97)	5.3 (6.38)	0.588
Turbidity (m)	0.57 (0.28)	0.62 (0.36)	0.475
Distance to Canopy Tree (m)	7.7 (10.38)	9.3 (9.68)	0.398
Submerged Vegetation (%)	5.6 (10.98)	2.7 (1.15)	0.000
Floating Vegetation (%)	5.9 (9.74)	5.8 (18.58)	0.987
Canopy Closure (%)	71.8 (35.19)	61.9 (34.81)	0.154

Table 6. Descriptive statistics of morphological measurements from 35 *Macroclmys temminckii* caught between May 1996 and August 1999.

		Female	Male	Juvenile	Summary
	N	9	17	9	35
Mass (kg)	Mean	17.3	18.6	3.9	14.4
	Max	25.5	36.7	9.5	36.7
	Min	6.5	7.3	0.7	0.7
	Standard deviation	6.6	9.9	2.2	9.9
Midline carapace length (cm)	Mean	41.1	41.8	24.4	36.9
	Max	46.9	55.0	33.5	55.0
	Min	31.6	31.2	14.5	14.5
	Standard deviation	5.5	7.1	4.8	9.8
Shell width (cm)	Mean	34.6	36.1	20.4	31.8
	Max	41.1	47.3	23.8	47.3
	Min	28.3	27.9	12.7	12.7
	Standard deviation	4.4	5.8	3.7	8.3
Shell depth (cm)	Mean	15.7	16.2	9.1	14.2
	Max	20.4	20.2	10.7	20.4
	Min	11.4	12.1	5.3	5.3
	Standard deviation	2.9	2.4	1.8	3.9
Skull width (cm)	Mean	12.6	13.3	7.6	11.7
	Max	16.2	18.7	8.6	18.7
	Min	10.1	10.2	4.9	4.9
	Standard deviation	2.1	2.3	1.2	3.1

Table 7. Means and p-values from statistical tests of differences between occupied microhabitats and random microhabitat sites.

		Mean	Standard deviation	N	Test statistic	p
<b>Individuals</b>						
DFS (distance from shore)	OS	3.98 m	0.33 m	11	T = -6.73	<0.05
	RS	7.09 m	1.44 m			
DFT (distance from tree)	OS	3.97 m	0.32 m	11	T = -9.40	<0.05
	RS	7.28 m	1.15 m			
DPTH (depth)	OS	2.85 m	0.24 m	11	T = -0.40	0.69
	RS	2.90 m	0.33 m			
LOGS (log size)	OS	2.86	0.36	11	Z = -2.93	<0.05
	RS	0.78	0.33			
LOGC (log complexity)	OS	2.42	0.21	11	Z = -2.94	<0.05
	RS	0.84	0.41			
<b>Pooled</b>						
DFS	OS	4.03 m	0.70 m	169		
	RS	7.16 m	1.38 m	169		
DFT	OS	3.97 m	2.70 m	169		
	RS	7.33 m	3.91 m	169		
DPTH	OS	2.85 m	0.70 m	169		
	RS	2.89 m	1.38 m	169		
LOGS	OS	2.85	1.23	169		
	RS	0.76	1.49	169		
LOGC	OS	2.40	0.97	169		
	RS	0.77	0.67	169		

Table 8. Descriptive statistics for water temperature at microhabitat sites occupied (OS) by individual *M. temminckii* and randomly chosen sites (RS).

Subject ID#	Mass	n	Occupied sites		Random sites	
			min – (mean) – max variance	min – (mean) – max variance		
21	15.25	14	10.3 – (15.94) – 24.4 34.21	10.4 – (16.29) – 27.5 47.88		
26	8.20	18	10.6 – (17.56) – 29.0 45.03	10.2 – (16.72) – 26.4 40.43		
28	17.50	21	9.9 – (18.59) – 28.2 53.87	10.1 – (16.45) – 30.0 38.26		
30	11.25	14	20.3 – (26.64) – 29.6 4.89	17.2 – (22.87) – 32.2 20.93		
36	10.50	10	10.4 – (11.17) – 12.7 0.70	10.2 – (11.31) – 14.0 1.34		
37	27.50	5	10.4 – (11.34) – 13.6 1.78	10.0 – (10.36) – 10.9 0.11		
39	17.75	18	20.6 – (24.86) – 29.5 8.61	16.7 – (22.32) – 29.4 15.64		
47	21.50	13	20.6 – (24.95) – 28.9 8.62	18.4 – (25.32) – 35.4 33.22		
51	21.50	10	10.2 – (11.29) – 12.6 0.88	10.0 – (10.97) – 13.9 1.41		
74	17.25	15	21.5 – (25.32) – 28.7 4.39	19.1 – (24.06) – 30.9 16.78		
77	15.00	20	19.2 – (24.15) – 27.5 6.51	16.2 – (22.51) – 33.4 25.45		
Pooled		158	9.9 – (20.37) – 29.6 45.91	10.0 – (19.06) – 35.4 46.20		
Averaged			14.9 – (19.26) – 24.1 15.41	13.5 – (18.11) – 25.8 21.95		

Table 9. Descriptive statistics of  $T_b$  and  $T_a$  from 4 *Macroclmys temminckii* in the field.

	Month								
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Total
<b><math>T_b</math></b>									
$\bar{x}$	27.76	27.37	25.16	20.71	14.67	12.21	12.24	13.13	19.96
min	24.07	22.38	21.04	15.17	11.57	8.97	9.44	11.45	8.97
max	31.27	32.62	30.13	25.63	20.43	16.12	16.59	17.39	32.62
variance	1.78	1.96	2.39	5.41	3.12	2.91	2.72	1.66	39.22
n (turtles)	1	3	3	4	3	3	1	1	4
n (measurements)	960	5400	5400	4710	5400	3260	1860	1614	28604
<b><math>T_a</math></b>									
$\bar{x}$	27.76	27.12	24.93	20.36	14.25	11.69	11.89	12.82	19.63
min	20.74	16.67	17.79	14.8	11.38	8.60	9.06	11.23	8.60
max	38.17	38.07	30.8	25.87	21.02	15.91	16.86	18.31	38.17
variance	4.35	3.21	3.17	5.69	3.36	3.30	3.51	2.17	41.01
n (turtles)	1	3	3	4	3	3	1	1	4
n (measurements)	960	5400	5400	4710	5400	3260	1860	1614	28604

Table 10. Means, variances, and heating and cooling rates ( $\tau$ ) for subjects in the field.

Turtle ID	Mass	Mean Tb	Mean Ta	Tb variance	Ta variance	Heating $\tau$	Cooling $\tau$
37	27.50	20.98	20.62	26.01	27.14	52.56	139.2
34	10.50	21.27	20.96	32.26	33.29	47.15	119.92
30	11.25	26.93	26.81	2.65	4.12	62.56	86.94
21	15.25	13.41	13.00	6.45	6.97	66.20	128.77
Summary	16.13	20.65	20.34	16.84	17.88	57.12	118.70

Table 11. Cooling rates ( $\tau$ ) for 5 *Macrolemys temminckii* subjected to a 14 °C change (32 °C – 18 °C).

Turtle ID	Mass (kg)	minutes	Thermal Time Constant ( $\tau$ )
101	0.70	27.75	6.62
24	3.50	89.00	13.69
22	4.25	91.50	29.49
52	7.00	175.00	36.02
33	26.25	326.00	116.58

Table 12 Comparison of habitat variables at turtle relocation points (n = 66) and random points (n = 43) in the Stephen F. Austin Experimental Forest.

HABITAT VARIABLE	TURTLE RELOCATION POINTS (MEAN, SE)	RANDOM POINTS (MEAN, SD)	P
Turtle Depth (m)	1.27 (0.36)	0.79 (0.43)	0.000
Water Depth w/in 5 m (m)	1.30 (0.29)	1.03 (0.52)	0.002
Stream Width (m)	5.33 (2.31)	3.63 (2.54)	0.001
Distance to Shore (m)	1.40 (1.18)	0.94 (0.74)	0.032
Turbidity (m)	0.58 (0.23)	0.48 (0.12)	0.201 n.s.
Diameter Nearest Log (m)	45.3 (23.92)	30.2 (16.86)	0.020
Submerged Vegetation (%)	0.19 (1.35)	0.59 (2.52)	0.308 n.s.
Floating Vegetation (%)	2.64 (12.72)	2.02 (8.27)	0.787 n.s.
Canopy Closure (%)	738.27 (1447)	83.44 (12.70)	0.065 n.s.
Distance Nearest Canopy Tree (m)	9.5 (11.39)	6.1 (3.55)	0.069 n.s.
Diameter Nearest Canopy Tree (cm)	43.4 (15.02)	39.8 (11.01)	0.205 n.s.

Figure 1.

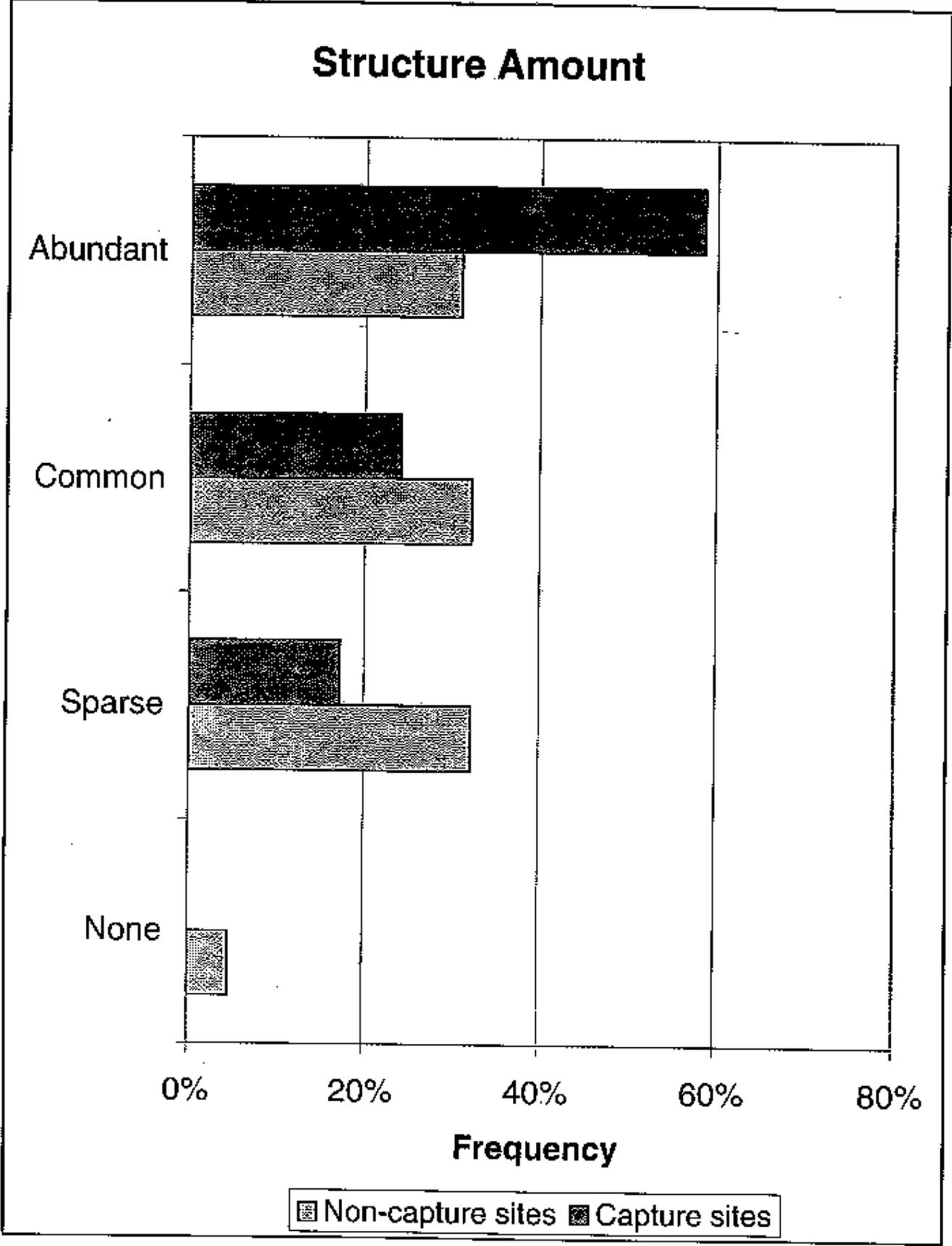


Figure 2.

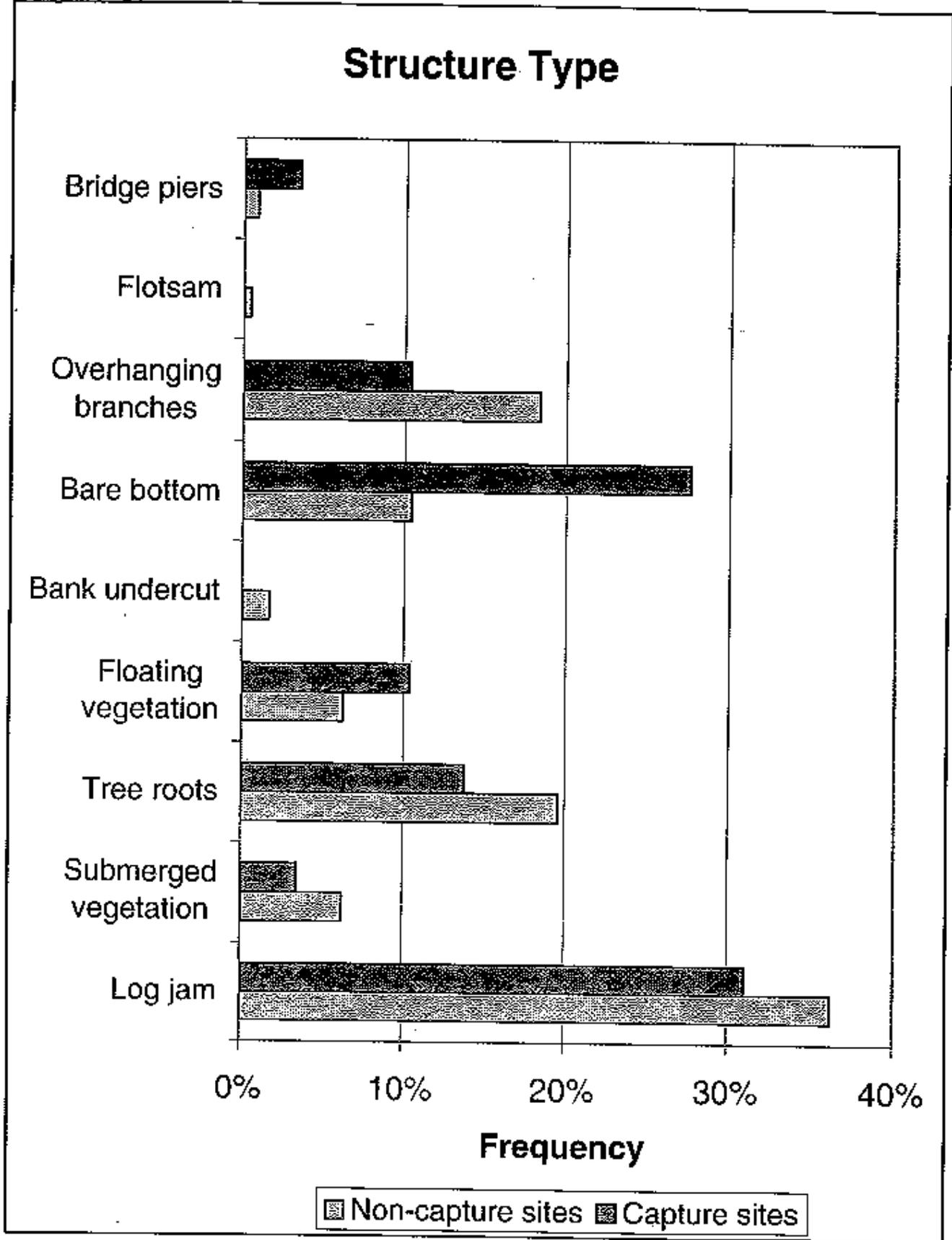


Figure 3.

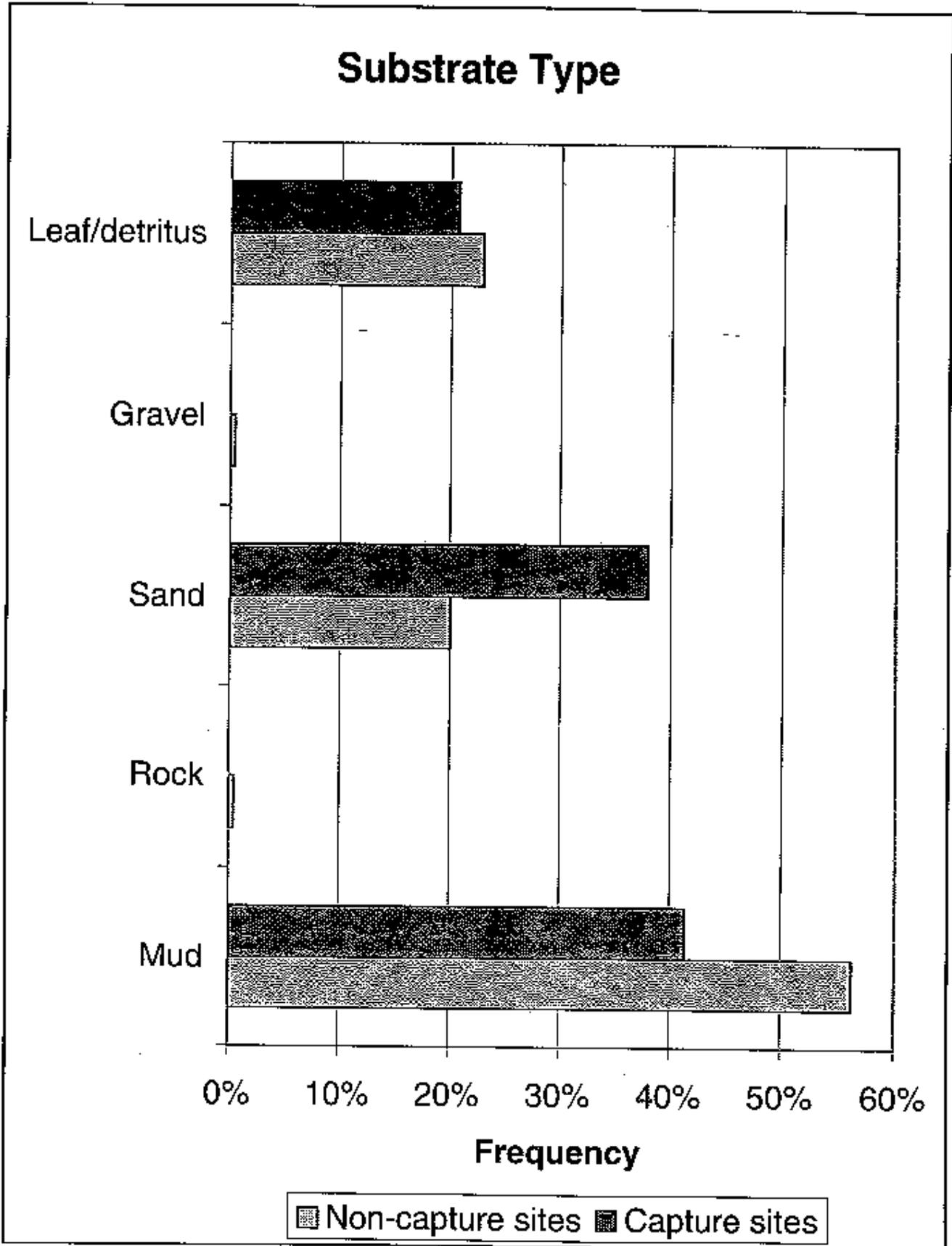


Figure 4.

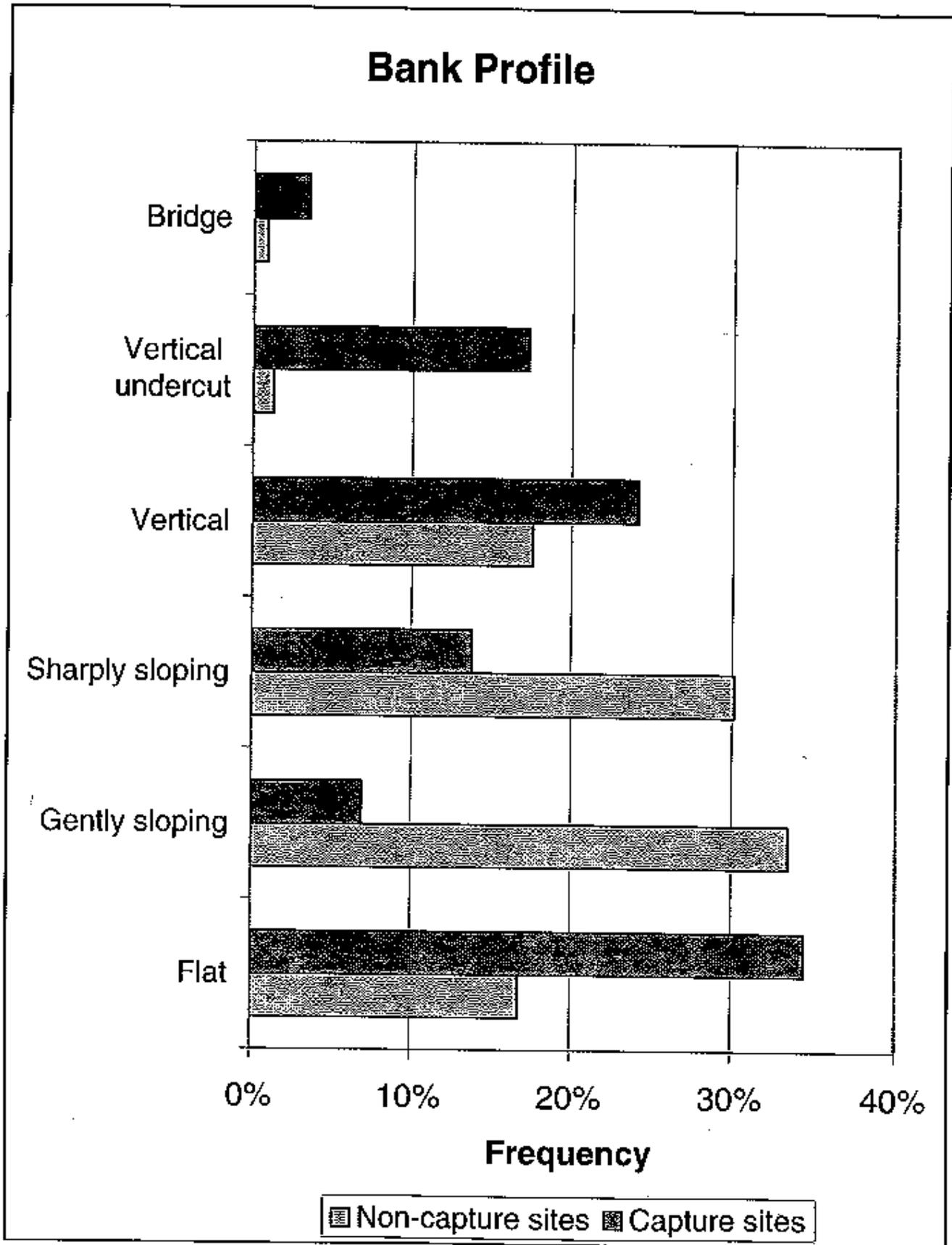
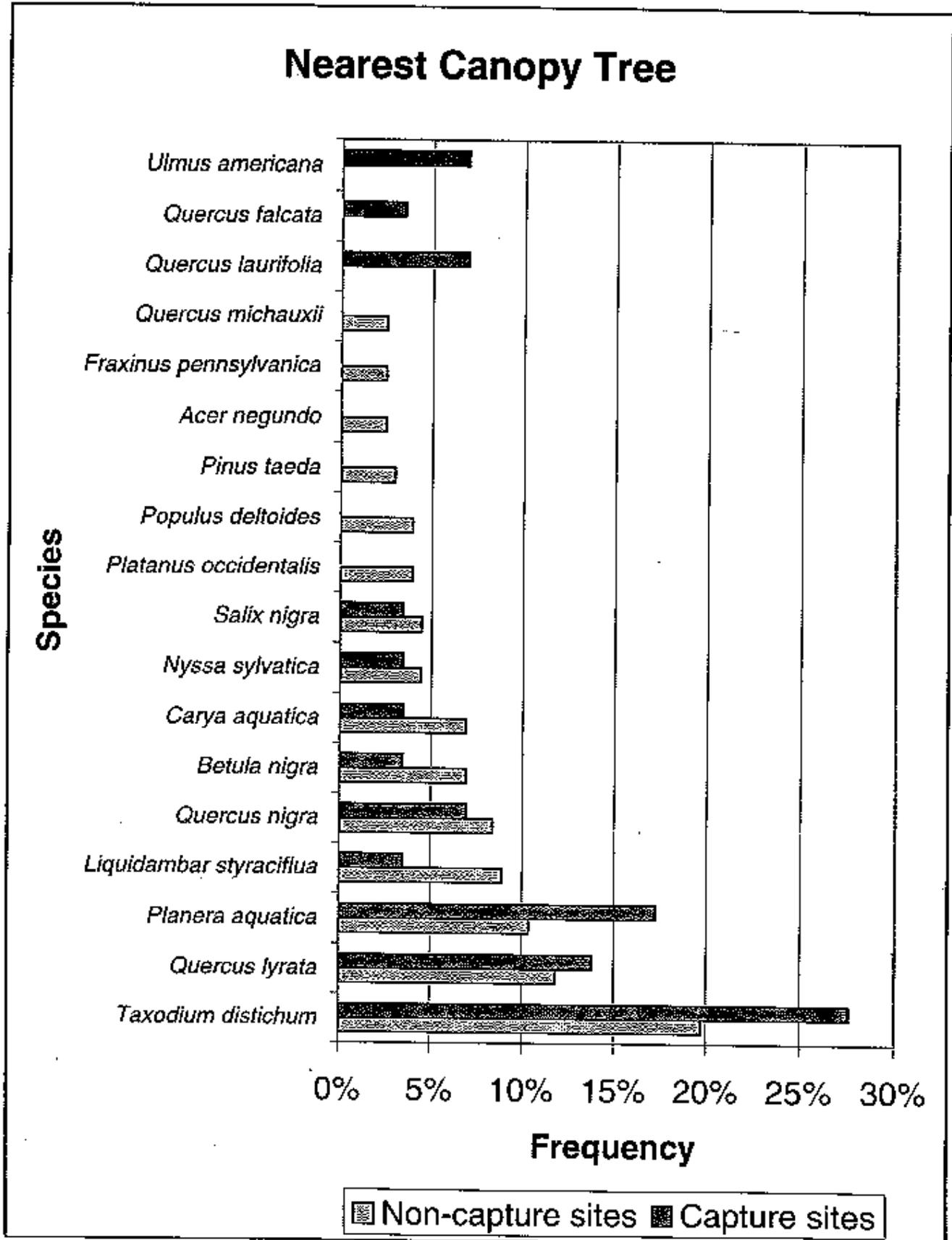


Figure 5.



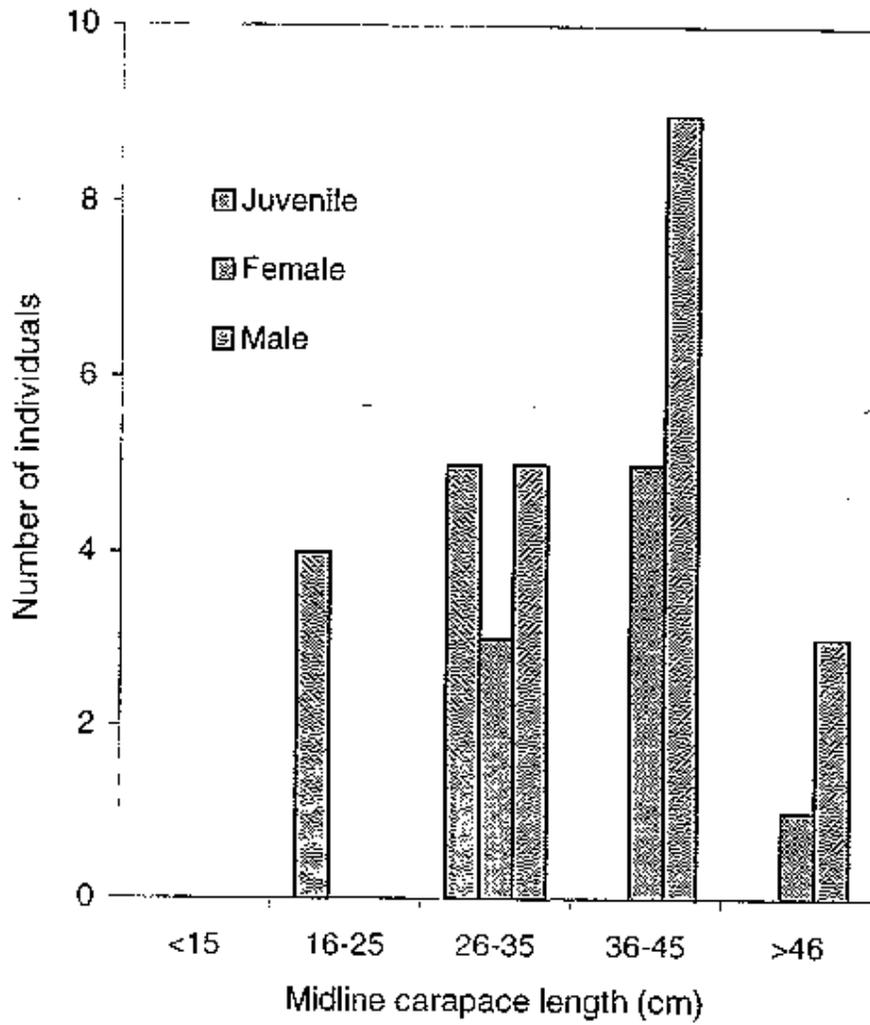


Figure 6. Size distribution of *Macrocllemys temminckii* caught in Bingham Lake, Tyler County, Texas.

Figure 7. Examples of  $T_b$  and  $T_a$  from two Alligator Snapping Turtles in the field. Solid lines represent  $T_b$  and dashed lines represent  $T_a$ .

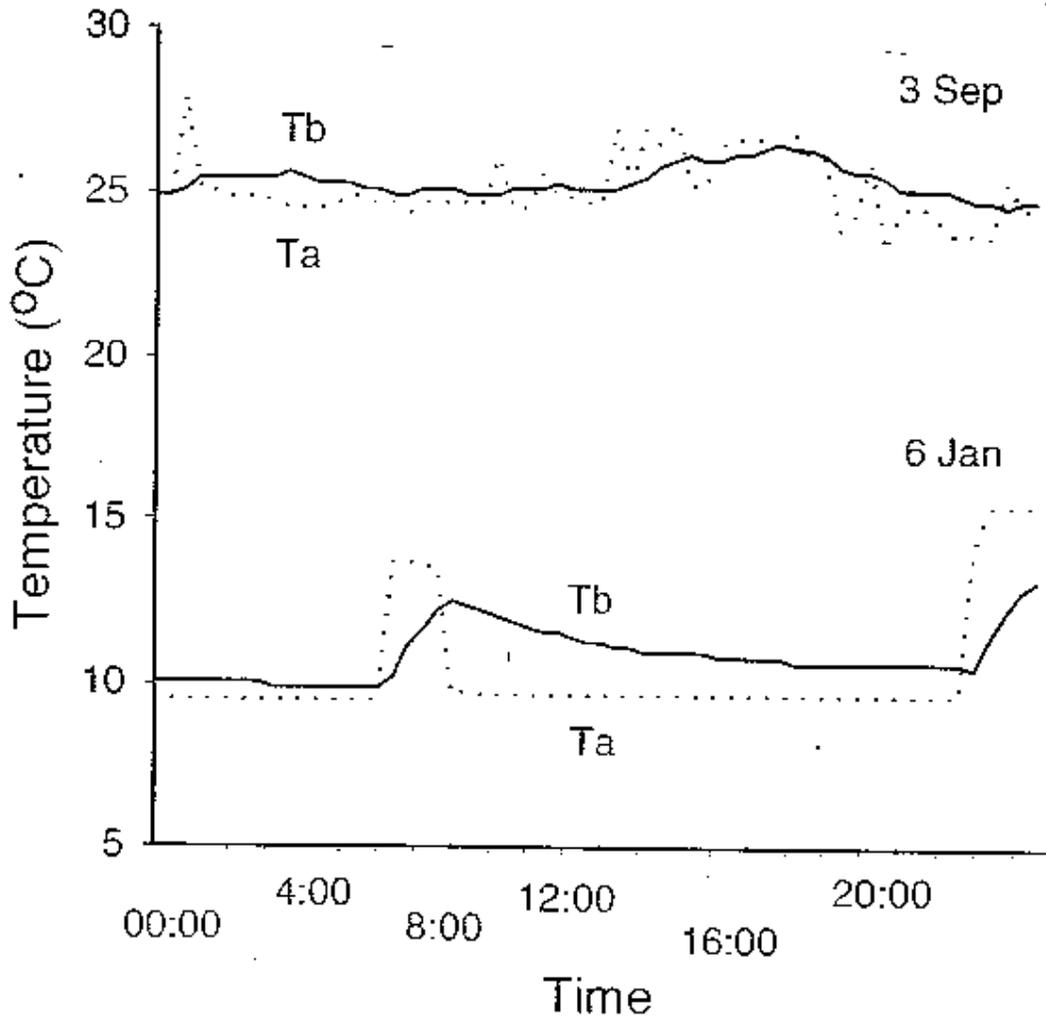


Figure 8. Autocorrelograms of sequential differences between  $T_b$  and  $T_a$  from four *M. temminckii* in the field.

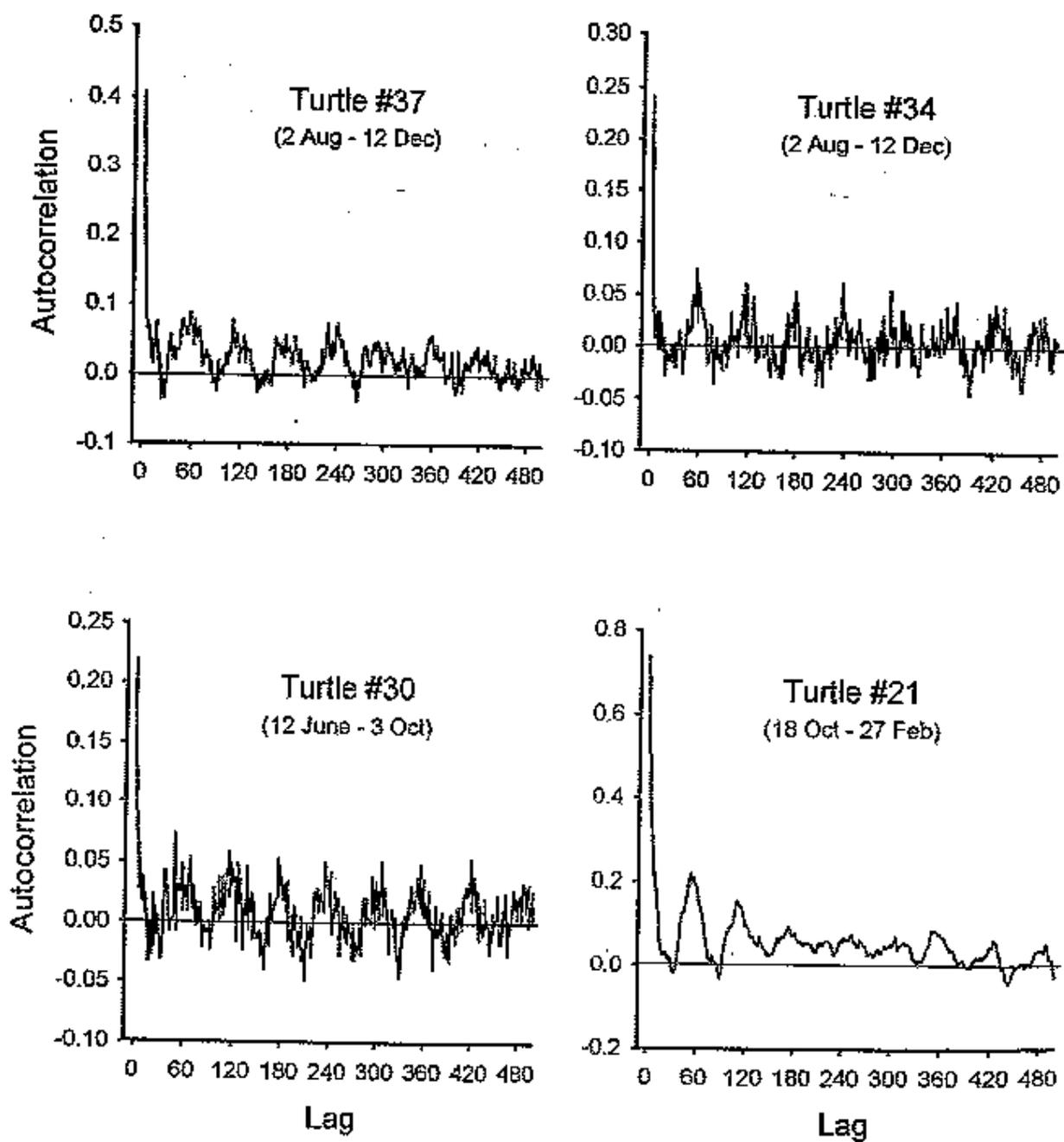


Figure 9. Mean daily body temperatures of Alligator Snapping Turtles for each month.

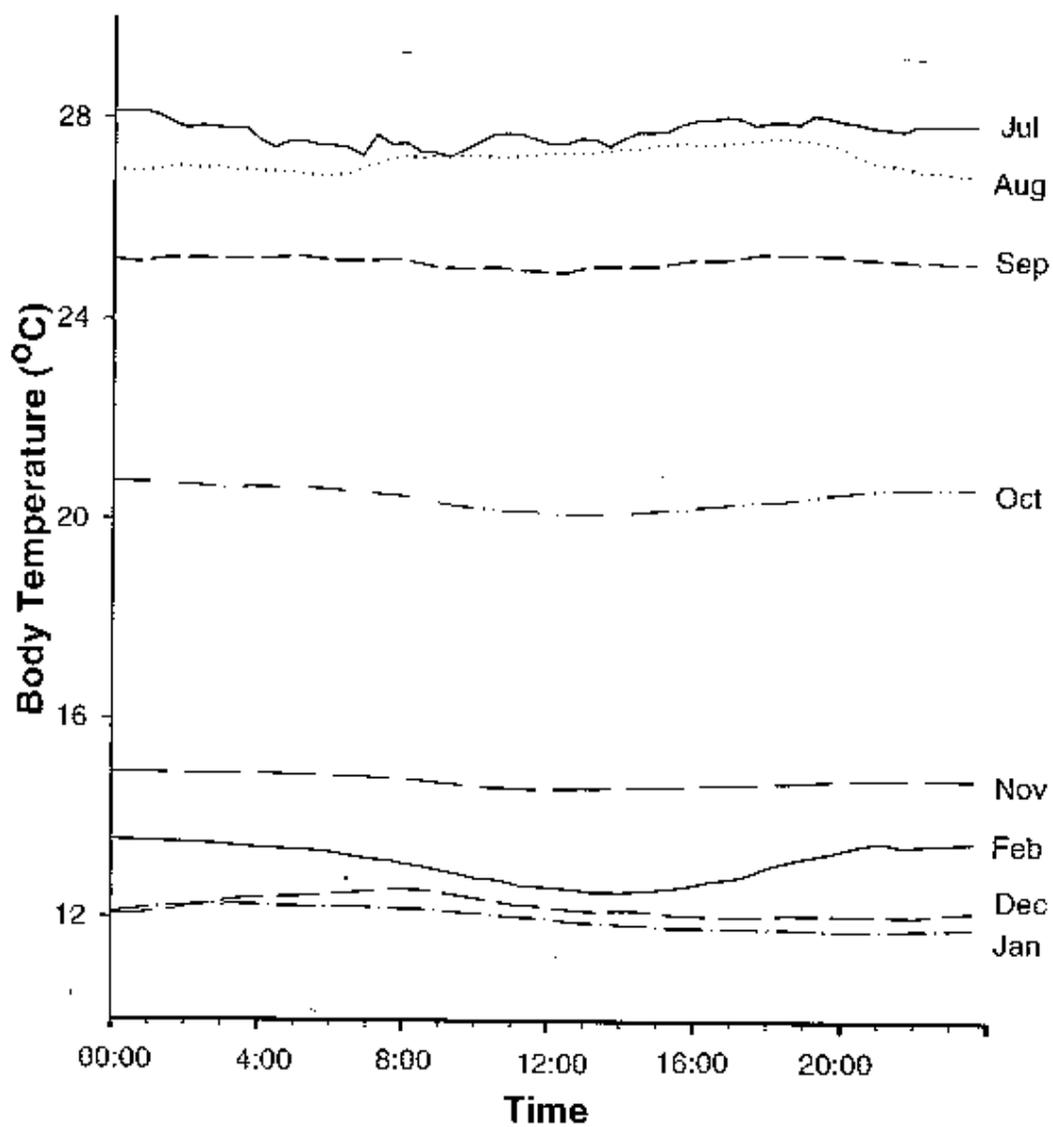


Figure 10. Scattergrams of  $T_b$  vs  $T_a$  for four Alligator Snapping Turtles in the field. Regression lines are solid. Dashed lines show a slope of 1 ( $T_b = T_a$ ).

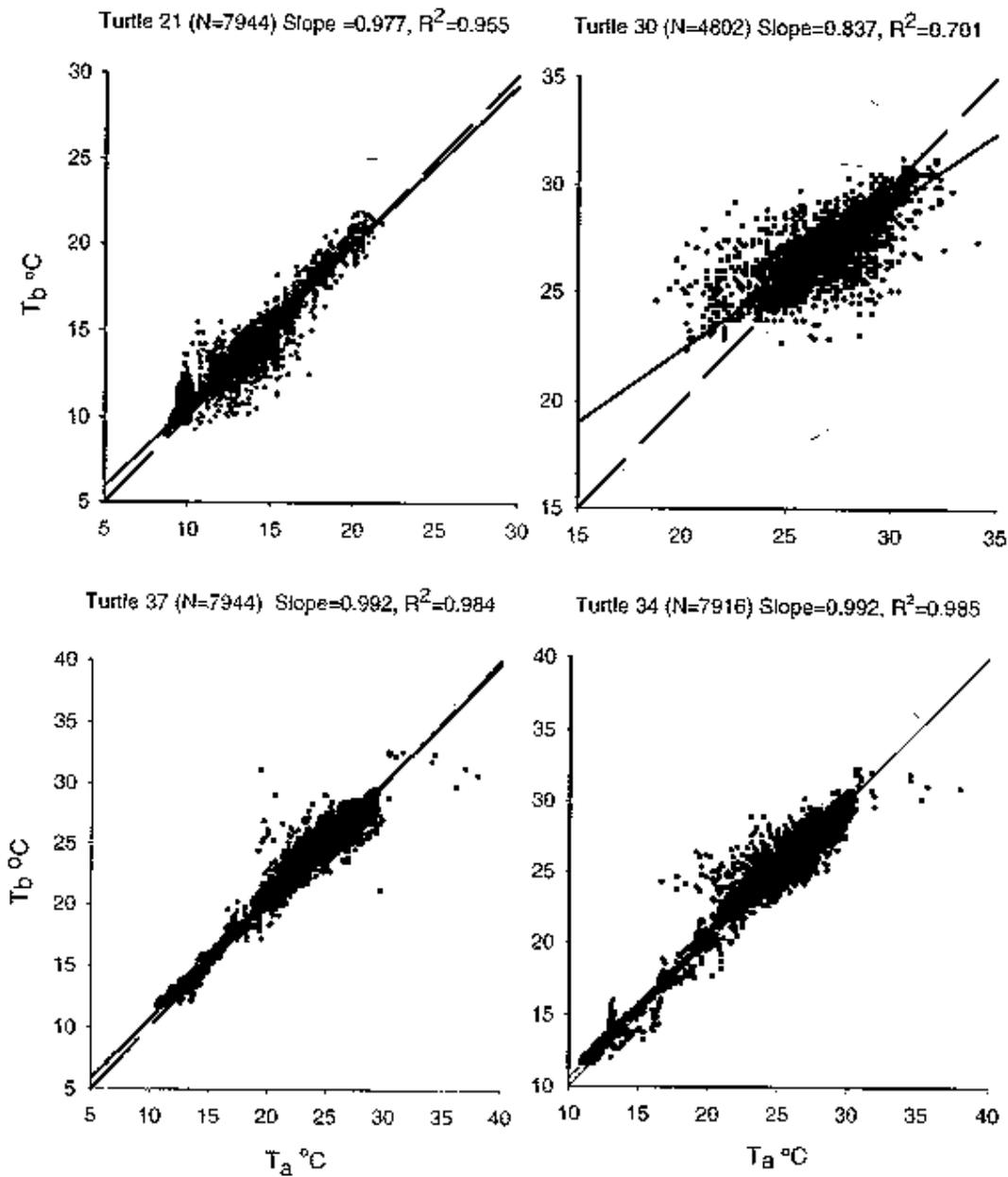


Figure 11. The relationship between cooling time constants and turtle mass.

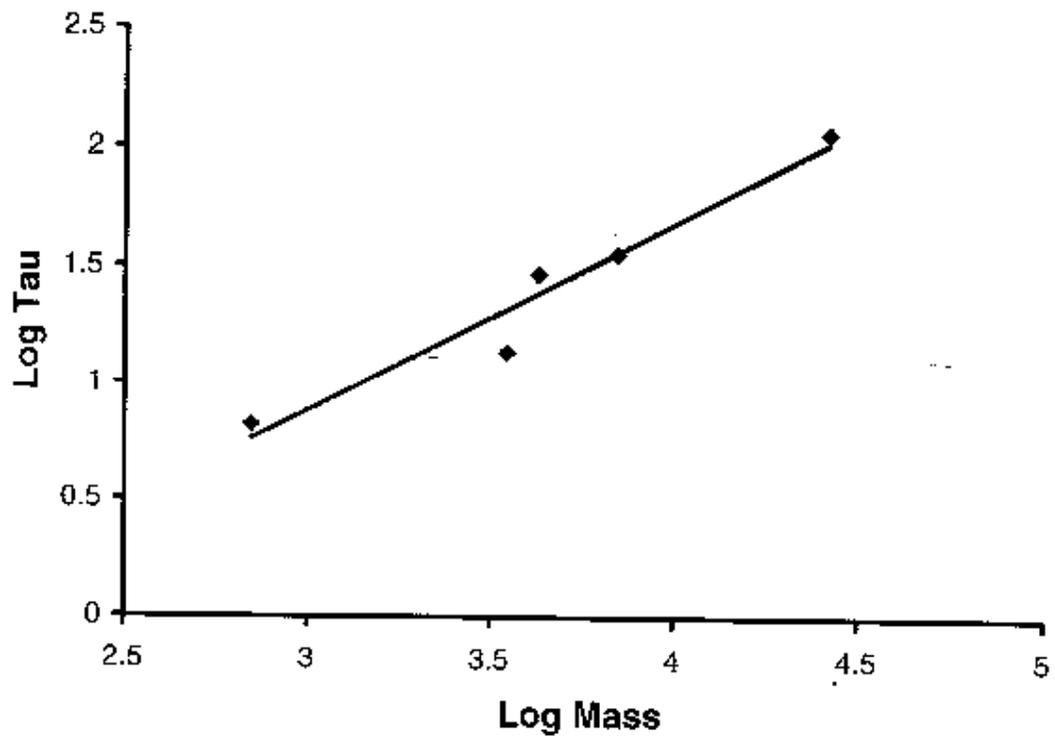


Figure 12

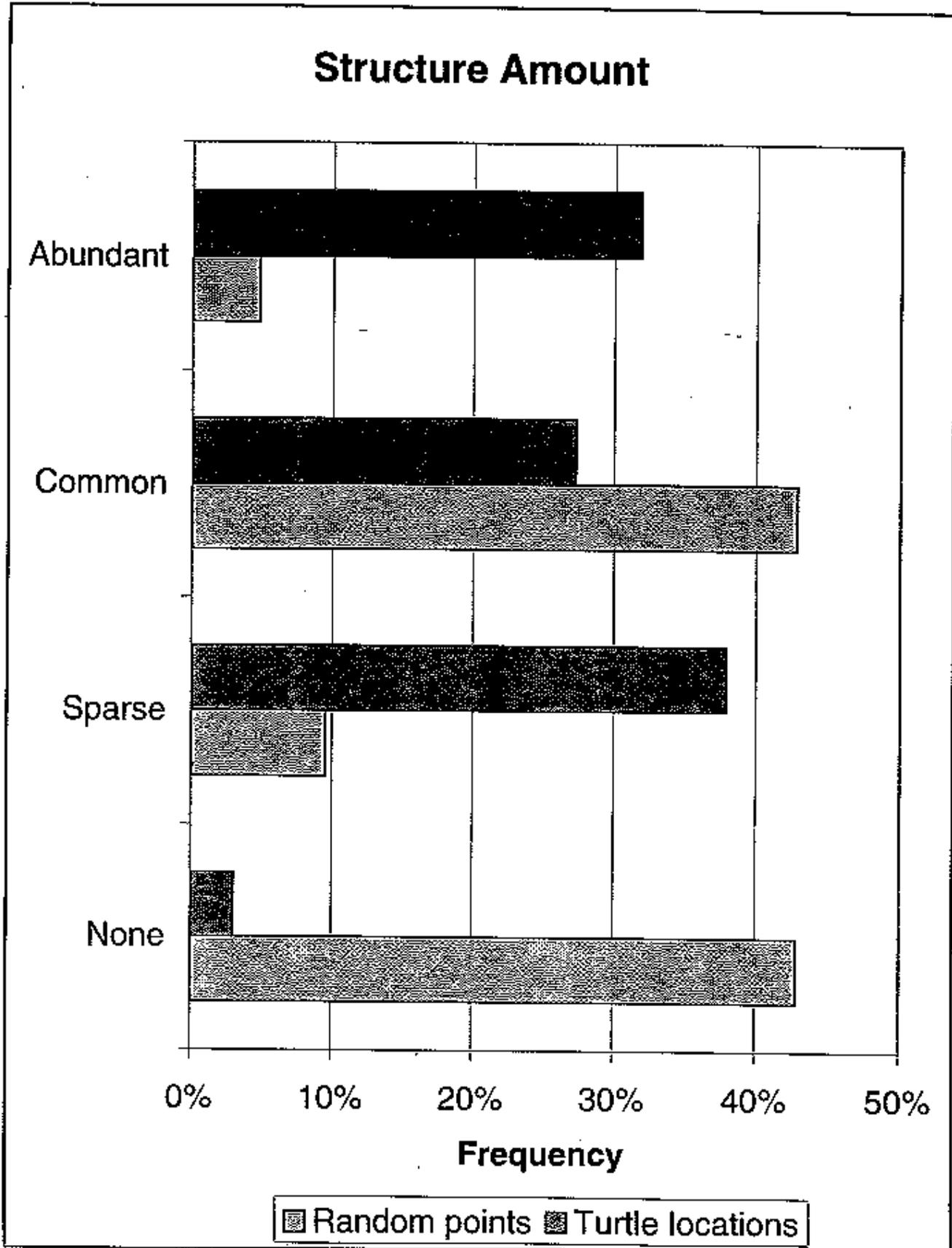


Figure 13

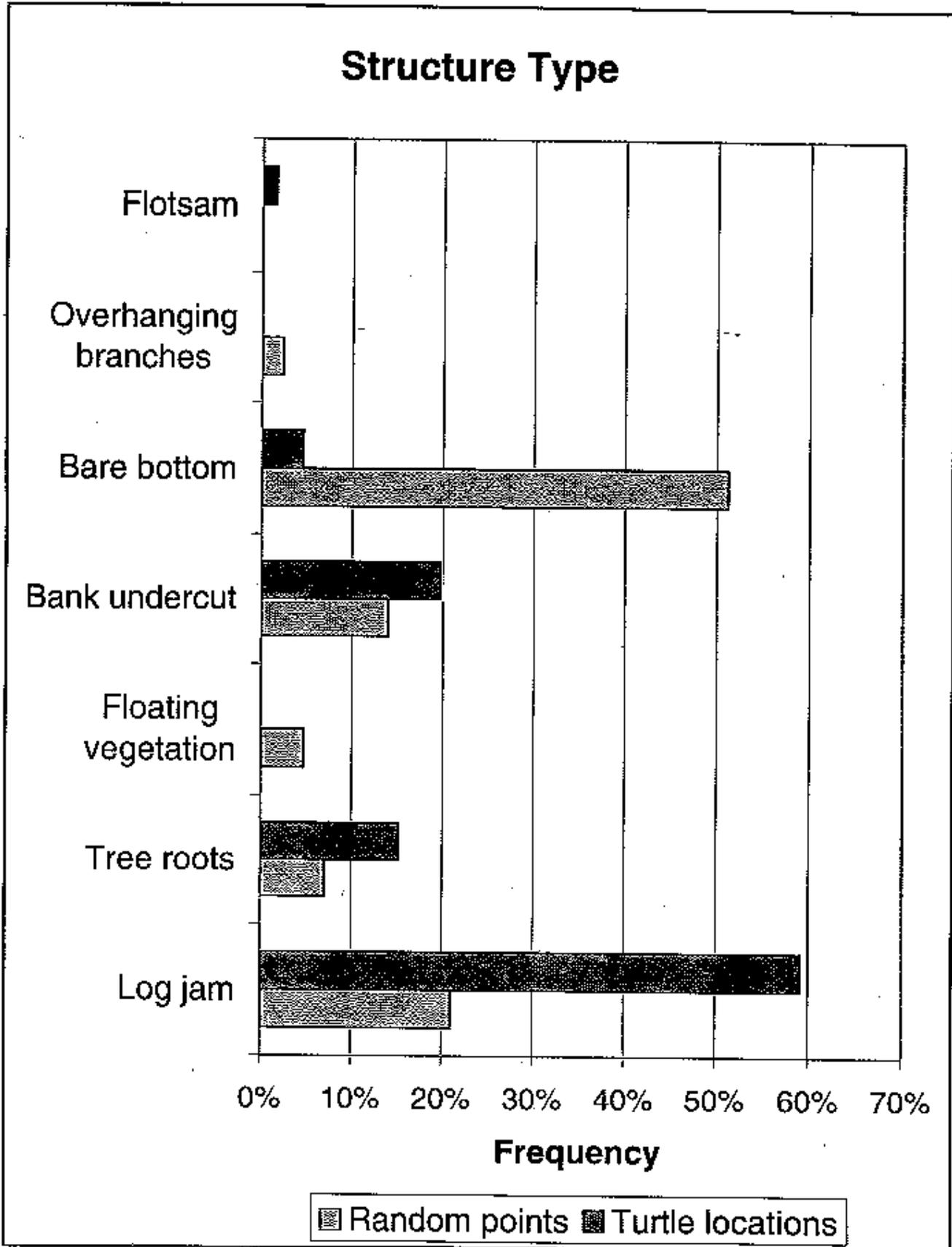


Figure 14

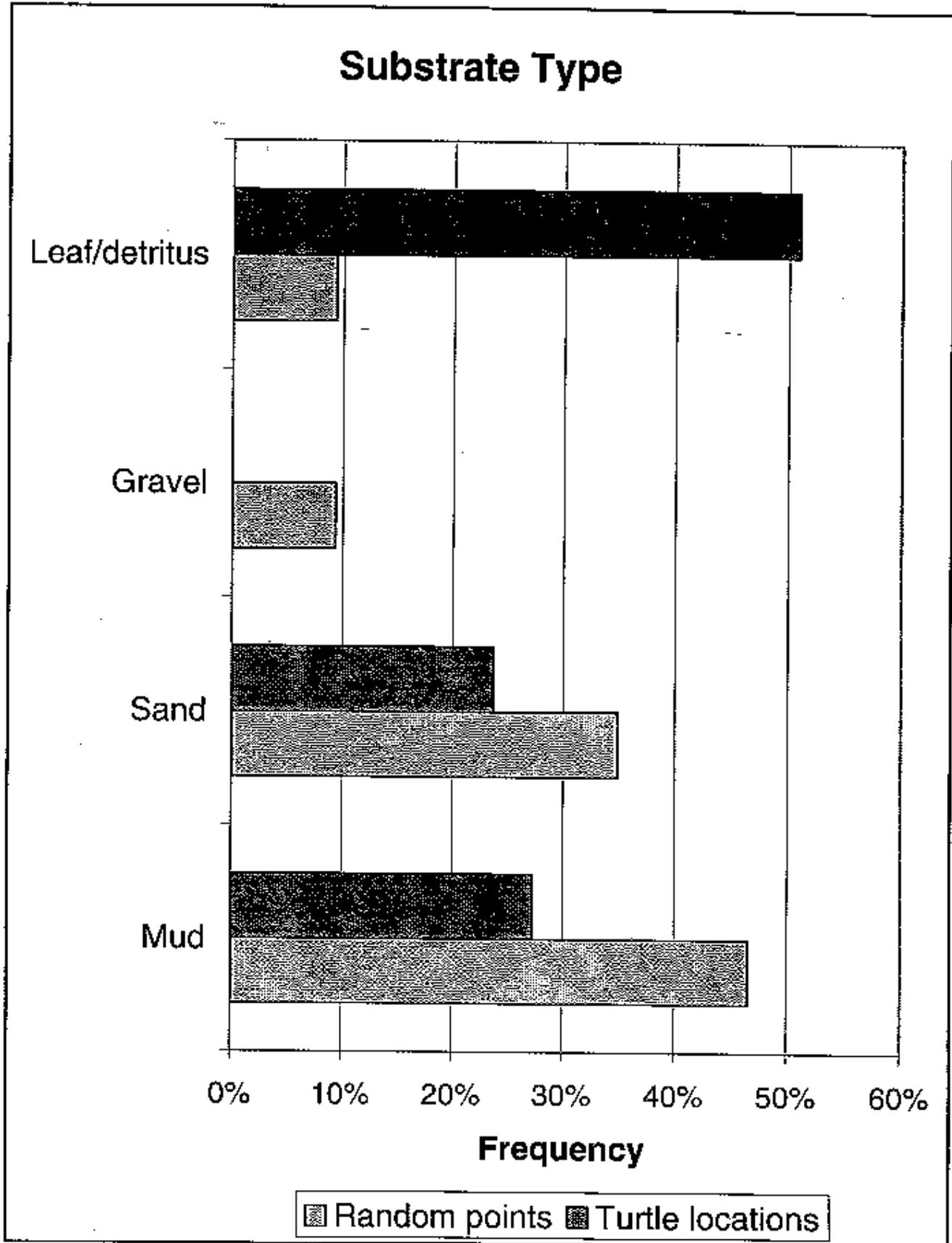
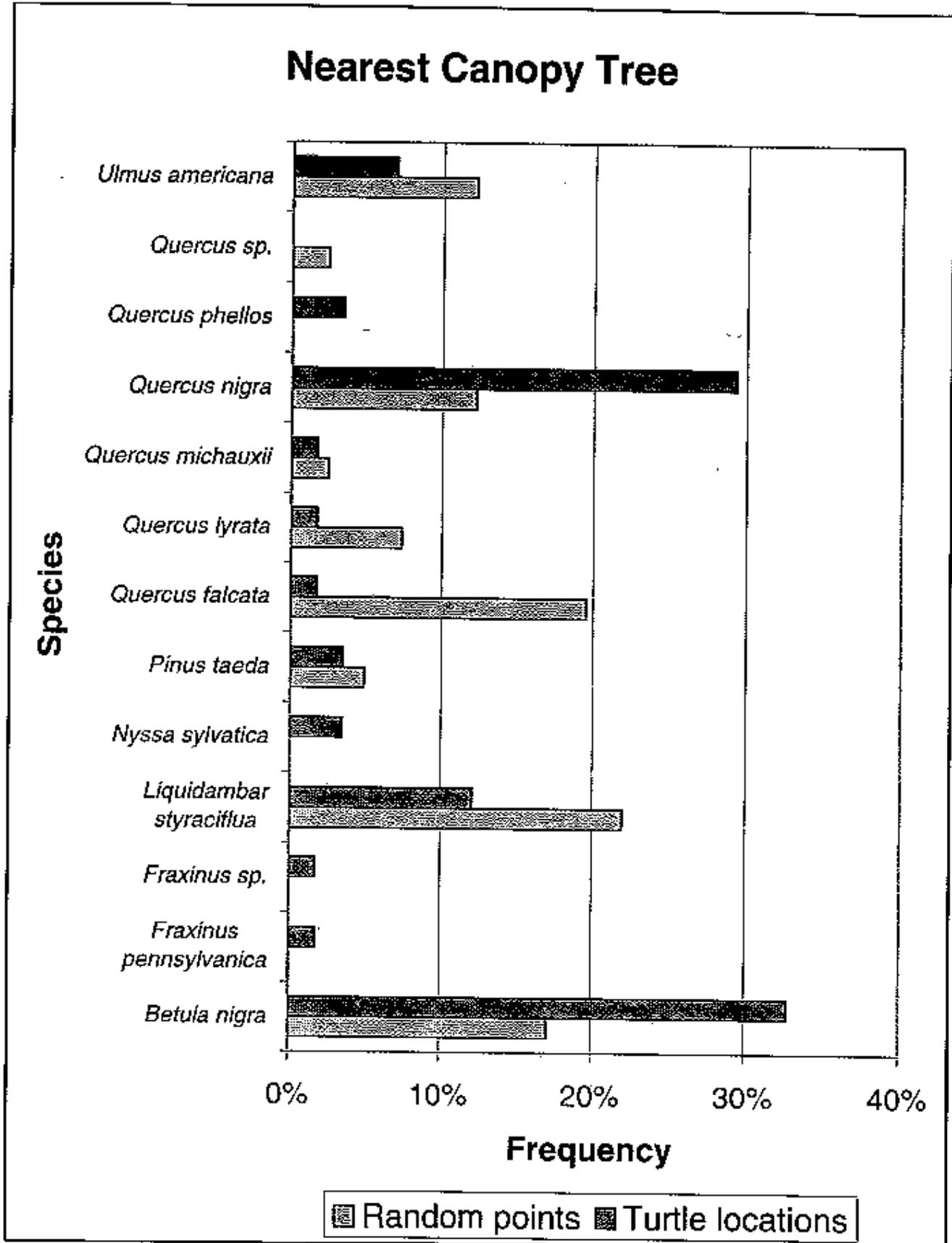


Figure 15



Appendix 1. Alligator snapping turtle capture data for Texas.

DRAINAGE	SITE	DATE	SEX	CARAPACE LENGTH (cm)	MASS (kg)		
Sabine	Lost Creek	18 Oct. 2000	F	35.1	10.2		
			F	39.0	12.3		
	Swede Johnson Bayou	16 Aug. 2001	Juv.	27.0	4.7		
			Juv.	29.0	5.0		
			Juv.	28.9	6.0		
			M	45.5	22.5		
	Beaver Lake	20 July 1999	M	49.5	25.5		
			M	31.0	7.0		
			F	45.5	21.0		
			F	41.7	16.6		
			F	42.6	18.0		
	Lake Fork	14 June 2001	F	42.6	18.0		
			M	43.7	21.0		
			M	47.9	27.5		
Cypress	Caddo Lake	16 May 2001	M	57.6	46.5		
			M	52.1	34.2		
			M	47.9	27.5		
			F	36.4	12.0		
			M	54.2	42.0		
			F	40.3	16.0		
Angelina	Angelina River	27 Ap. 1999	F	36.3	11.5		
			Bonaldo Creek	19 July 2000	F	45.4	23.8
					F	45.4	21.5
					F	40.3	18.0
					M	52.9	36.5
Neches	Bingham Lake	24 Aug. 1999	M	52.3	30.5		
			Juv.	15.5	0.8		
	Old Neches Lake	14 May 2001	F	43.0	19.5		
			M	57.2	41.3		
			M	42.0	16.8		
			F	42.0	16.7		
			Juv.	28.0	5.8		
			F	39.9	14.0		
	West Fork San Jacinto River	17 June 2001	M	41.2	16.2		
			Juv.	20.9	1.9		
			Juv.	26.0	4.2		
Trinity	Pickett's Creek	26 July 2000	Juv.	26.0	4.2		
			Catfish Creek	9 June 1999	F	39.2	14.3
					F	40.3	15.7
		10 June 1999	Juv.	25.8	4.1		

	Keechi Creek	14 June 1999	M	38.3	12.8
			M	35.4	10.5
			M	58.2	38.5
			M	30.4	6.8
			M	37.1	11.0
			F	46.1	21.3
			F	44.3	19.3
		15 June 1999	F	42.6	17.5
Trinity	Trinity River, Collin Co.	15 Aug. 2002	M	58.3	46.4