NATURAL HISTORY OF *TERRAPENE COAHUILA*, A RELICT AQUATIC BOX TURTLE IN NORTHERN MEXICO

by

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ABSTRACT

An ecological study of a relict population of the unique aquatic box turtle, Terrapene coahuila, has revealed that population densities, foraging behavior, food habits, and thermal relationships of this species more closely resemble other North American aquatic turtles than terrestrial members of its own genus. Coahuilan box turtles inhabit small, spring-fed marshes of dense aquatic vegetation in an interior basin of the Chihuahuan Desert in central Coahuila, on the northern Mexican Plateau.

T. coahuila occurs in considerably higher numbers and is restricted to smaller areas of activity than its terrestrial congeners, T. carolina and T. ornata. Sixty turtles per acre is typical of the marshes studied. Its population density is comparable to aquatic emydines, such as Chrysemys picta.

Mating occurs from September to June and is most concentrated in March and April. Egg laying begins in late April and continues to late September; clutches of 2 or 3 eggs are most common. About half of the females can produce second clutches, and about one-third lay three sets annually. These females produce a mean of 6.8 eggs/female per season, a higher reproductive potential than in

northern populations of Terrapene, and reversing the latitudinal cline of lower reproductive potentials in southern than in northern turtle populations.

T. coahuila is opportunistic and omnivorous, closely resembling other aquatic or semiaquatic turtles in feeding extensively on aquatic plants and insects, and in foraging with the head underwater.

In the warm southern and thermal-spring environment, activity is extended; T. coahuila is often active in shallow water of marshes during winter, despite low air temperatures. Water and body temperatures were nearly identical at all seasons, as are those of other aquatic turtles while in water. In summer temperatures fluctuated drastically with time of day.

Danger of extinction is real. Main threats to the existence of the species are destruction of aquatic habitats by artifical draining, and over-collecting by curious amateurs.

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INTRODUCTION

Of the four living species of box turtles (genus Terrapene: Testudinidae, Emydinae) now recognized, only the isolated Coahuilan Box Turtle, Terrapene coahuila Schmidt and Owens, is aquatic. Known only from an interior desert basin of about 800 km^2 located near Cuatro Ciénegas de Carranza, Coahuila, on the Central Plateau of northern Mexico, T. coahuila represents today an aquatic-adapted, endemic population surrounded by a vast, arid desert region. As ecological studies of relict populations are few, and the turtle is so unique, it seemed appropriate to learn as much as possible about its habits and adaptations, and to compare this information with that on other aquatic emydines and with data on terrestrial species of Terrapene. This paper reports results of laboratory and field study of the Coahuilan Box Turtle in the period December 1964 through October 1966.

The basin of Cuatro Ciénegas became known to biologists through the discovery by E. G. Marsh, Jr. in 1939 of several of its endemic vertebrates. Terrapene coahuila was one of the first new species described in 1944 from Marsh's collections, but many endemic forms have been discovered in the last several years from more recently-obtained material. New fishes and aquatic reptiles that have been described are the following: Gambusia longispinis (Minckley, 1962), Xiphophorus gordoni (Miller and Minckley, 1963), Lucania interioris (Hubbs and Miller, 1965), Pseudemys scripta taylori (Legler, 1960a), and Trionyx ater (Webb and Legler, 1960). Vertebrate endemism and reliction in the basin have been summarized briefly by Milstead (1960), Hubbs and Miller (1965), and Taylor and Minckley (1966). Minckley (unpublished manuscript, 1967) has reviewed extensively known information concerning the geology, physiography, climate, aquatic habitats, drainages, and biota of the Cuatro Ciénegas basin. Among invertebrates, Taylor (1966) described 12 new endemic species of hydrobiid snails (Gastropoda) from the basin. These were classified in five new endemic genera and three new endemic subfamilies. Reviewing this remarkable assemblage of mollusks, Taylor (1966:214) states: "The small valley of Cuatro Ciénegas . . . has yielded the most spectacularly endemic fauna of freshwater snails known in the Western Hemisphere." Of six crustaceans known from the basin, one is an endemic subterranean isopod, Speocirolana thermydronis, described by Cole and Minckley (1966), and another is an undescribed isopod of the family Shaeromidae which is probably endemic and may represent a new genus (Minckley, unpublished manuscript, 1967). Fragmented specimens of the undescribed sphaeromid were in stomach contents of a female T. coahuila (ASU 05876) collected 31 July 1965 in posa 11 (Fig. 8), 10 km southwest of Cuatro Ciénegas (see "Study Area").

The genus *Terrapene* has been reviewed by Milstead and Tinkle (1967), who recognize two natural divisions, the Ornata and the Carolina species groups. Living forms of the Ornata group are as follows: *T. ornata ornata* of central USA; *T. o. luteola* of southwestern United States, and Chihuahua and Sonora, Mexico; *T. nelsoni nelsoni* of Nayarit, Mexico; and *T. n. klauberi* of Sonora and Sinaloa, Mexico. The Carolina group encompasses the following: *T. carolina carolina* of eastern United States; *T. c. bauri* of Florida; *T. c. major* of extreme southern United States; *T. c. triunguis* of east-central United States; *T. c. mexicana*, of San Luis Potosí and Tamaulipas, México; *T. c. yucatana* of Yucatán and Campeche, Mexico; and *T. coahuila*.

Since the original description of *T. coahuila* by Schmidt and Owens (1944), the species has been mentioned in various papers on the fauna of the Cuatro Ciénegas basin. To date, the most significant contribution to our knowledge of the species is that of Webb, Minckley, and Craddock (1963). Their paper dealt with the different kinds of aquatic habitats in which Coahuilan Box Turtles were found, and provided notes on habits of the species and on its distribution in the basin. Brief references to *T. coahuila* were made by Hubbs and Miller (1965), Legler (1960a, 1960), McDowell (1964), Milstead (1956), Taylor

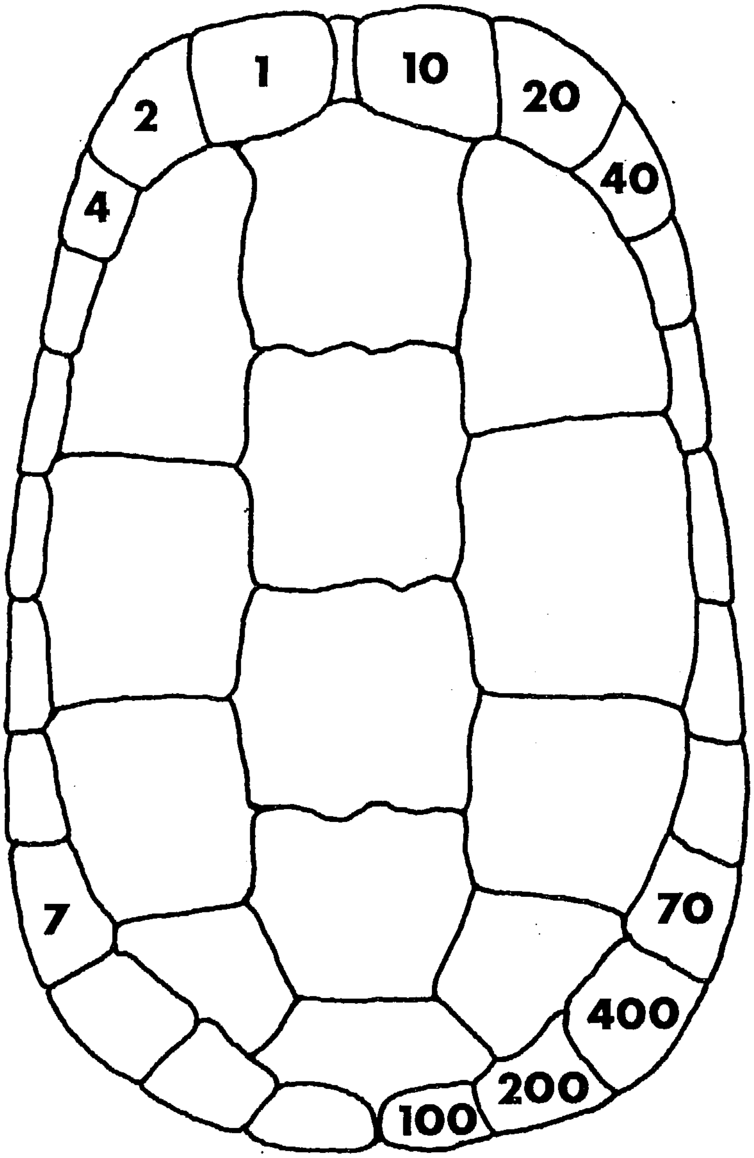
(1966), Williams (1960), Williams and Han (1964), Williams, Smith, and Chrapliwy (1960), and Zug (1966).

Terrapene coahuila was believed to be the most primitive member of the genus and the most closely allied to the ancestral stock of Terrapene by Auffenberg (1958) and Legler (1960a, 1960). Auffenberg and Milstead (1965), and Milstead (1960, 1967), however, have suggested that T. coahuila evolved from a disjunct remnant, or relict, population that became isolated during Pleistocene from a population of turtles inhabiting the eastern Gulf coast of México, and intermediate in morphology between the extinct T. c. putnami and the modern T. c. triunguis. Alternating north-south migrations of the Gulf coast population with each glacial and interglacial stage of the Pleistocene left disjunct populations of Terrapene in Yucatán and Campeche (T. c. yucatana), San Luis Potosí and Tamaulipas (T. c. mexicana), and Coahuila (T. coahuila) (Milstead, 1967). Milstead (1967:177) visualized rapid selection for aquatic existence ". . . in but a few thousand years . . ." in those Terrapene trapped within the Cuatro Ciénegas basin, where no intermediate mesic habitat exists between the marshes (where T. coahuila lives today) and the surrounding arid terrain. Milstead's argument would seem to be bolstered by the theoretical discussion of Mosimann (1958b: 256-257) who suggested that ". . . in an area of two habitats, where one is of much less spatial extent than the other, there could be an accelerated natural selection for a character of specific adaptation for the smaller habitat, by virtue of the necessity of the sparse species to maintain itself above a critical density." Taylor (1966:159) believed that the snail genus Mexipyrgus in the Cuatro Ciénegas basin may have been distinct since the early Tertiary, stating: "The possibility that there has been a freshwater habitat in the area continuously suitable for snails since middle or early Tertiary time should . . . be considered seriously." He inferred that speciation within the genus Mexipyrgus has taken place in the last 2 or 3 million years and that springs in the basin may also be of that age. Taylor (1966:160) stated further: ". . . the interpretation of evolution in fishes, reptiles, and other groups [in the Cuatro Ciénegas basin] should not rest merely on the assumption of a certain rate of differentiation, nor on inferred effects of climatic change during the Pleistocene." Many more data, biological and geological, are needed before the age and significance of T. coahuila, and the other extraordinary elements of the biota of the Cuatro Ciénegas basin, can be interpreted.

MATERIALS AND METHODS

The study area was visited, and field observations of Terrapene coahuila made, on the following dates: 28 - 31 December 1964, 14 April 1965, 2 July - 31 August 1965, 20 - 22 December 1965, 24 - 29 January 1966, 3 - 8 April 1966, 25 - 26 July 1966, 11 September 1966, and 14 - 15 October 1966. Box turtles were obtained by hand-collecting and marked by notching the marginal scutes of the carapace with a hacksaw blade following a code system shown in Fig. 1. Where possible, the exact location of capture was recorded for individuals in marshes; after mapping the marshes, capture locations were measured by pacing the distance from stakes placed around the perimeter. Routine procedure included marking and measuring each turtle; recording the location of capture, body and environmental temperature; the presence of ectoparasites, injuries, and markings; and the time of capture and general weather conditions. Turtles were measured in the field with large wooden calipers equipped with a millimeter ruler, and with vernier calipers. Descriptions of methods used in mapping marshes, measuring turtles, observing turtle activities, recording temperatures, and examining stomach contents and reproductive organs of preserved specimens in the laboratory are given under the appropriate

Figure 1. System of marking turtles.


1
10
2
20
4
40
7
70
400
200
100

headings in the text.

Specimens of T. coahuila examined in the laboratory are from the following collections: United States National Museum (USNM) 159578; University of Kansas Museum of Natural History (KU) 46917 - 46293, 51431, 51433 - 51436; and Arizona State University (ASU) 05853 - 05900, 08000 - 08001.

All mean values reported throughout this paper are followed by ± one standard error (SE).

GEOGRAPHICAL SETTING AND HABITAT

The Chihuahuan Desert covers the northern portion of the Mexican Plateau between the Sierra Madre Occidental on the west and the Sierra Madre Oriental on the east. It extends from approximately 21° to 33° north latitude and from 99° 108° west longitude, from Aguascalientes and northern Guanajuato in the south to southern New Mexico and southwestern Texas in the north, and from central Chihuahua, Durango, and Zacatecas in the west to east-central Coahuila and San Luis Potosí (Jaeger, 1957; Milstead, 1960). This area corresponds roughly with the Anahuac Desert Plateau physiographic province of Thayer (1916), and with the northern two-thirds of the Mexican Plateau, known as the Mesa del Norte (West, 1964).

The desert plateau ranges in elevation from apprxoimately 300 to 900 meters in the north to about 1,500 meters in the south and west (Goldman and Moore, 1945). Mountain ranges, ranging in elevation from 1,800 to 2,700 meters, are interspersed among plains and numerous interior basins, creating a rugged topography (Goldman and Moore, 1945; Milstead, 1960). West (1964:48) described the Mesa del Norte as ". . . a vast area of folded and faulted mountain ranges separated and half buried by deep deposits of alluvium that form extensive basin plains." Rainfall varies from 0 to approximately 400 mm annually in this arid region (Shreve, 1944; Leopold, 1950). Vegetation consists primarily of creosote bush desert, dominated by creosote bush (*Larrea divaricata*), tar-bush (*Flourensia cernua*), mesquite (*Prosopis* spp.), catclaw (*Acacia* spp.), hackberry (*Celtis* spp.), ocotillo (*Fouquieria splendens*), and cacti (*Opuntia* spp., and other genera). Less extensive major vegetation types are the cactus deserts, including various cacti, yuccas, and shrubs adjoining mesquite-grassland transition communities along the eastern base of the Sierra Madre Occidental, and the alkaline flats of interior basins, often supporting stands of tobosa, *Hilaria mutica* (Leopold, 1950).

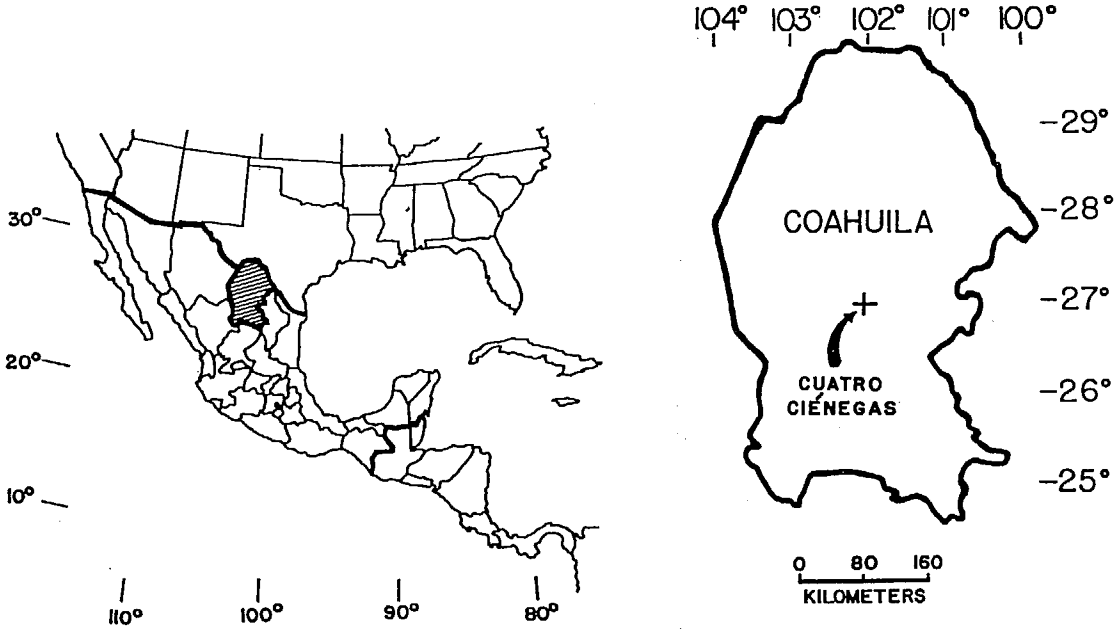
The topography and climate of Coahuila were summarized by Muller (1947) and Baker (1956). Three physiographic areas of the state can be recognized: the Gulf Coastal Plain, the mountains, and the desert plains of the Central Plateau. The major mountain ranges are extensions of the Rocky Mountain - Sierra Madre Oriental axis which extends from the northwestern to the southeastern portions of the state. This axis runs from the Sierra del Carmen range in northwestern Coahuila to the Sierra Madre Oriental in the southeast, including the Sierra Hermosa de Santa Rosa, the Sierra de la Madera, and the Sierra de San Marcos. Peaks reaching more than 2,700 meters are found in the Sierra del Carmen and the Sierra de la Madera, and peaks more than 3,000 meters occur in the Sierra Madre Oriental near the southeastern border of the state. Other discontinuous, north-south trending ranges are found west of the major montane axis, but most do not exceed 1,800 meters in elevation. These scattered ranges, along with buttes, low hills, and undrained basins, give the central plateau of western Coahuila its rugged topography. In southern Coahuila, east-west trending mountains extend from the Sierra Madre Oriental of southeastern Coahuila and Nuevo León to the Sierra Madre Occidental of Durango.

Climate of Coahuila is influenced primarily by its continental position and by effects of its mountain ranges (Muller, 1947). Most of the state is arid. Easterly winds from the Gulf of Mexico are blocked by the Sierra del Carmen axis, resulting in the high eastern mountains receiving most rainfall. Rainfall is moderate (200 - 600 mm) on the Coastal Plain, whereas the lowlands of the plateau in western Coahuila remain arid, having an annual rainfall of 0 to 200 mm (Shreve, 1944; Vivó Escoto, 1964).

Cuatro Ciénegas Basin

The basin of Cuatro Ciénegas lies at the eastern edge of the Chihuahuan Desert in central Coahuila, México (Fig. 2). The elevation at Cuatro Cienegas is 742 m; the town is at 26°58' north latitude, 102°04' west longitude (Contreras, 1942; Gilmore, 1947). The basin is located just inside the Chihuahua-Zacatecas Biotic Province of Goldman and Moore

Figure 2. Geographical location of Cuatro Ciénegas, Coahuila, Mexico.


30°
20°
10°
110°
100°
90°
80°
104°
103°
102°
101°
100°
-29°
-28°
-27°
-26°
-25°
COAHUILA
CUATRO CIÉNEGAS
0
80
160
KILOMETERS

(1945) and Stuart (1964) near its zone of contact with the Tamaulipas Biotic Province to the east. Along with plains and basins of western and southern Coahuila, the Cuatro Ciénegas basin belongs in the Chihuahuan Desert Shrub vegetation type of Muller (1947) and the Desert Scrub biotic community (biome) of Kendeigh (1954). The pass into the basin is an important break in the Sierra del Carmen - Sierra Madre Oriental axis, breaching the separation of the lowland Gulf Coastal Plain from the higher Central Plateau. Draining of the basin through this gap is by canals to the Río Salado de los Nadadores, which flows northeastward to be joined by the Río Sabinas and then into the Río Bravo del Norte (Río Grande). Gilmore (1947) gave a general description of the topography and habitats within the basin, and Webb et al. (1963) described the unique aquatic habitats in the basin, consisting mainly of streams, ponds, and marshes. Marshes were the habitat in which T. coahuila was investigated in this study.

The Cuatro Ciénegas basin is an expansive, grassy plain. It is approximately 25 km north to south by 40 km east to west, enclosed by the Sierra de la Madera (locally called Sierra de Anteojo) and Sierra de las Ovejas (locally called Sierra del Muerto) on the north, Sierra de San Marcos and Sierra de los Alamitos on the south, and surrounding ranges of the Sierra Madre Oriental on the east (Sierra de la Purisima and Sierra de San Vicente) and west (Sierra de la Fraqua, and Sierra de Jora). Sierra de San Marcos extends finger-like for about 20 km into the basin from the south, effectively dividing the basin into eastern and western lobes. Except for its bountiful springs and marshes, the basin is similar to the description of basins of southern and western Coahuila as described by Muller (1947). These generally have a level plain (barrial) surrounded by gently sloping bajadas from the nearby mountains. In many of the larger bolsones of the central and northern portions of the Chihuahuan Desert, tobosa flats, comprised of stands of Hilaria mutica, are characteristic of the vegetation on the bolson floor. These large llanos (grass covered bolson plains) receive little runoff from the surrounding mountains and may have only a small central playa (Muller, 1947), or may lack such a playa (Shreve, 1942). Typical desert shrub vegetation often occurs along the surrounding slopes of such llanos, and Shreve (1942:198) regarded the grassy vegetation as ". . . a desert association controlled by soil conditions." Shreve (1942) did not consider these llanos as true grassland, although they may appear as such. True climatic grassland is found in areas receiving relatively greater rainfall at higher elevations (1,800 to 2,000 meters), primarily along the eastern base of the Sierra Madre Occidental and in northern Coahuila at elevations of 1,500 to 1,800 meters (Shreve, 1942). The Cuatro Ciénegas basin, consisting of desert grass associations affected by edaphic conditions, has a large, shallow interior lake (laguna), several playas, and alkaline flats capable of holding shallow water during rainy periods. The basin floor consists largely of a light-colored alkaline soil corresponding to the alkaline desert soil type, one of four major classes of soils in Coahuila recognized by Muller (1947). Baker (1956:130) states ". . . near Cuatro Ciénegas a vast intermontane valley is overlain with glistening gypsum (anhydrite)." Although areas of large gypsum dunes occur in portions of the basin, gypsum deposits are not nearly as extensive as he implied. Webb et al. (1963:89) noted that the floor of the basin ". . . is mostly a surface layer of travertine or marl that is 2 to 8 feet in thickness and is rarely covered by more than 2 feet of overburden." In such basins, Muller (1947) noted that the saline lagunas are often surrounded by dropseed (<u>Sporobolus</u> spp.), saltbush (<u>Atriplex</u> spp.), iodine bush (<u>Allenrolfea</u> spp.), seepweed (<u>Suaeda</u> spp.), and mesquite (<u>Prosopis</u> spp.). These plants are all relatively salt-tolerant, and most are characteristic components of the vegetation in parts of the Cuatro Ciénegas basin.

<u>Study Area</u>

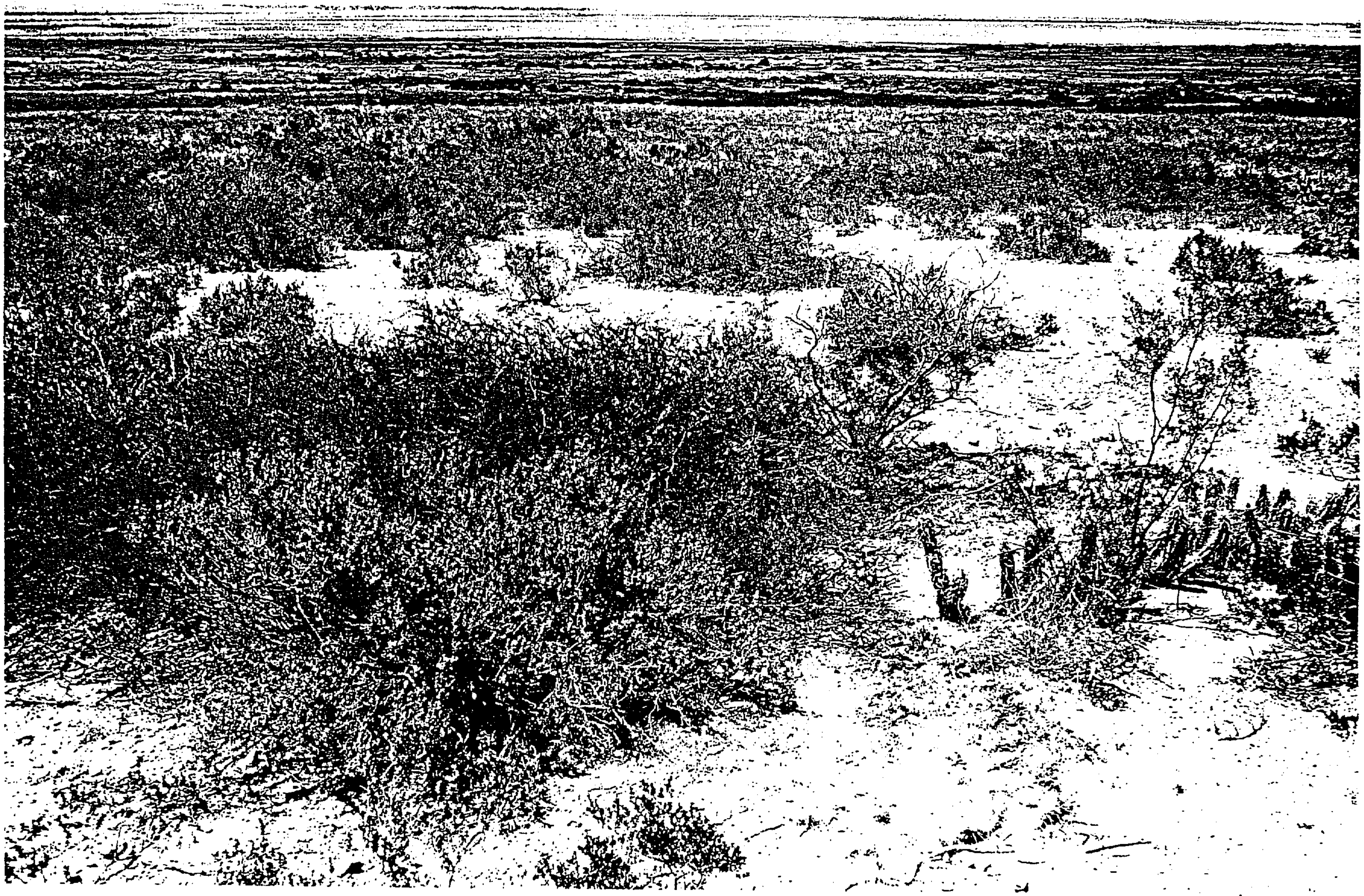
An area located approximately 10 km almost due southwest (224° from magnetic north) of the town of Cuatro Ciénegas was chosen for intensive field work. It is a gently-sloping grass zone immediately below the rocky bajada slope of the northeast tip of Sierra de San Marcos. By road, the area is 1.1 km south of the junction of the main road to San Pedro de las Colonias with a road following the east side of Sierra de San Marcos. This junction joins the main road 11.1 km southwest of Cuatro Ciénegas at the tip of the mountain.

The area was first visited on 30 December 1964. On that day and the next, 18 _T. coahuila_ were marked and released in a series of small, spring-fed marshes scattered within a region covering approximately 0.1 km^2 (25 acres). This area was deemed suitable for investigation since it was easily accessible, and since box turtles seemed present in sufficient numbers for a mark-recapture study.

Approaching the study area from the lower side of the bajada of Sierra de San Marcos, one finds a coarse, rocky soil sparsely covered with vegetation. Perhaps 30 to 40% of the ground surface is covered with woody shrubs and cacti. Mesquite, _Prosopis juliflora_, growing in low (1 m) thickets between 2 and 4 m in diameter, is the most conspicuous plant. Second in apparent abundance is seep-weed, _Suaeda fruticosa_, an indicator of saline soils. Scattered creosote bushes, _Larrea divaricata_, and cacti, _Opuntia_ spp., make up the remainder of the major plants along the lower edge of the bajada (Fig. 3).

Transition from the lower bajada to the grassy flats

Figure 3. View northeast toward study area from bajada slope at northern tip of Sierra de San Marcos. 12 July 1965. Plants include *Suaeda fruticosa* (left foreground); *Larrea divaricata* and *Opuntia* sp. (right foreground); and *Prosopis juliflora* (left center and background).



farther north is abrupt. The soil changes to a loose, bleached, travertine type with a fine texture, often becoming soft and spongy after a rain. Halophytic grasses, particularly an unidentified salt grass, Distichlis sp., growing in clumps, and a smaller, non-clumped species, Distichlis stricta, are prominent in the study area. Small patches of iodine bush, Allenrolfea occidentalis, are also abundant. Thick stands of marsh grass, Spartina spartinae, and drop-seed, Sporobolus airoides, are found in less extensive areas. Sporobolus grows in tussocks on slight rises within the farther-ranging Distichlis flats. Bare areas, sparsely covered with small aggregations of Distichlis, scattered clumps of Prosopis and catclaw (Acacia greggii), and patches of Allenrolfea, are occasionally encountered. This basin floor plant association, mainly consisting of various species of salt-tolerant grasses and shrubs, is found over the entire study area (Fig. 4). Portions are strikingly similar to the Distichlis stricta - Sporobolus airoides and Distichlis stricta - Allenrolfea occidentalis grassland communities occurring near spring-fed salt marshes in a desert basin in Utah as described by Bolen (1964).

As moist, spring-fed drainage areas are approached, slight local subsidence of the basin floor is evident. Bulrushes, Scirpus olneyi, and spike-rushes, Eleocharis rostellata, along with scattered clumps of saw grass, Cladium californicum, usually mark these wet regions.

Figure 4. Basin floor in study area, 28 July 1965. Plants include *Prosopis juliflora* (left center), *Distichlis* spp. and other grasses (foreground), and *Allenrolfea occidentalis* (right center and background). Note bare areas of bleached soils.

All marshes in the study area are characterized by Eleocharis rostellata, approximately 50 - 70 cm tall. This sedge provides the major portion of the vegetative cover within a marsh, supplemented in many by thick, submersed, mats of stonewort, Chara spp. Scirpus olneyi is an abundant plant in several marshes (Fig. 5). In marsh 2-A, bulrushes are dispersed without noticeable zonation among the more abundant Eleocharis, which makes up an estimated 70% of the marsh cover. In Utah, Bolen (1964:148) described boggy meadows of dense (1,720 stems/m^2) Eleocharis rostellata, ". . . an entangled and distinctive community", near the edges of major emergent-marsh communities dominated by Scirpus olneyi (263 stems/m^2).

Other species of plants occur frequently in and around the marshes or grow near them. One of these is seep-willow, Baccharis glutinosa, which commonly fringes a marsh, usually along the northern border. Seven of 11 marshes in the area of intensive study had one or more clumps of Baccharis along them (Fig. 6). Seep-willow could be seen from a distance and marked some of the marshes which would have been difficult to locate otherwise. The sedge, Fimbristylis thermalis, and sawgrass, Cladium californicum, are less common plants of the marshes. Distichlis stricta is usually found near moist areas close to a drainage channel or a marsh, and occasionally occurs on raised patches within a marsh.

Figure 5. Northeast view of marsh 2-A, 28 July 1965; habitat of *Terrapene coahuila*. Marsh vegetation consists of *Scirpus olneyi* and *Eleocharis rostellata*. Scattered *Spartina spartinae* and *Cladium californicum* occur at north end of marsh. Surrounding grasses are largely *Distichlis stricta*. Marsh 2 is at right center just before bare area; *Mojarral lagunas* are visible in background.

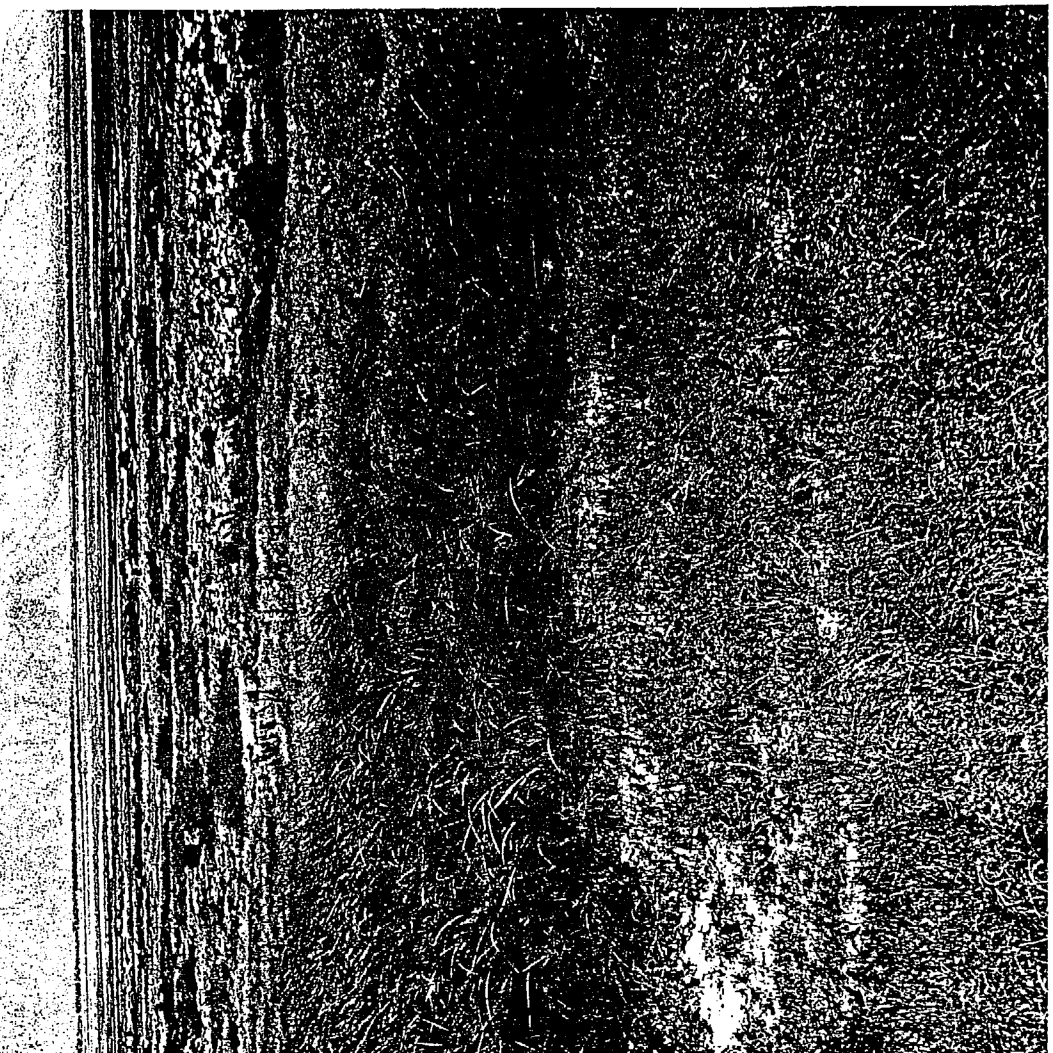


Figure 6. Northeast view of marsh 5, 28 July 1965, habitat of Terrapene coahuila. Marsh vegetation consists mainly of Eleocharis rostellata with Baccharis glutinosa around edges. Surrounding grasses are largely Distichlis stricta. Stakes around marsh perimeter were for mapping purposes.

The distinctness of the marshes from surrounding, halophytic grass associations is remarkable. The border of a marsh ends abruptly as it meets the slightly raised, dry, or seasonally water-logged, saline soil around it. During winter, the lush marsh vegetation is distinct from the brown grasses of the basin floor. Sharply-defined ecotones between Distichlis grasslands and marsh vegetation in a Utah basin were called "knife-edge community boundaries" by Bolen (1964:164).

Eleven marshes in the study area were visited regularly, and several others infrequently. The last marshes were approximately 0.8 km east of the study area. Ten marshes in the study area were mapped in the field with a Gurley transit; one was not mapped, but its size was estimated. Field locations along the perimeter of a marsh were plotted on graph paper from a reference point, and an outline map of each marsh was made (Fig. 7). From these maps, the area of each marsh was calculated with a planimeter, and checked by square counts; areas are given in Table 1. Maximum lengths range from 13 to 130 m, and maximum widths from 7 to 100 m. The largest (11; 8,745 m^2) is more than 150 times larger in area than the smallest marsh (6; 56 m^2) and more than 35 times larger than the mean area (227 m^2) of the ten smaller marshes. The largest marsh observed by Webb et al. (1963:93) ". . . did not exceed an area of about 500 square yards [ca. 418 m^2]."

Figure 7. Outline maps of 10 marshes in the study area. Marshes are arranged from smallest (left) to largest (right).

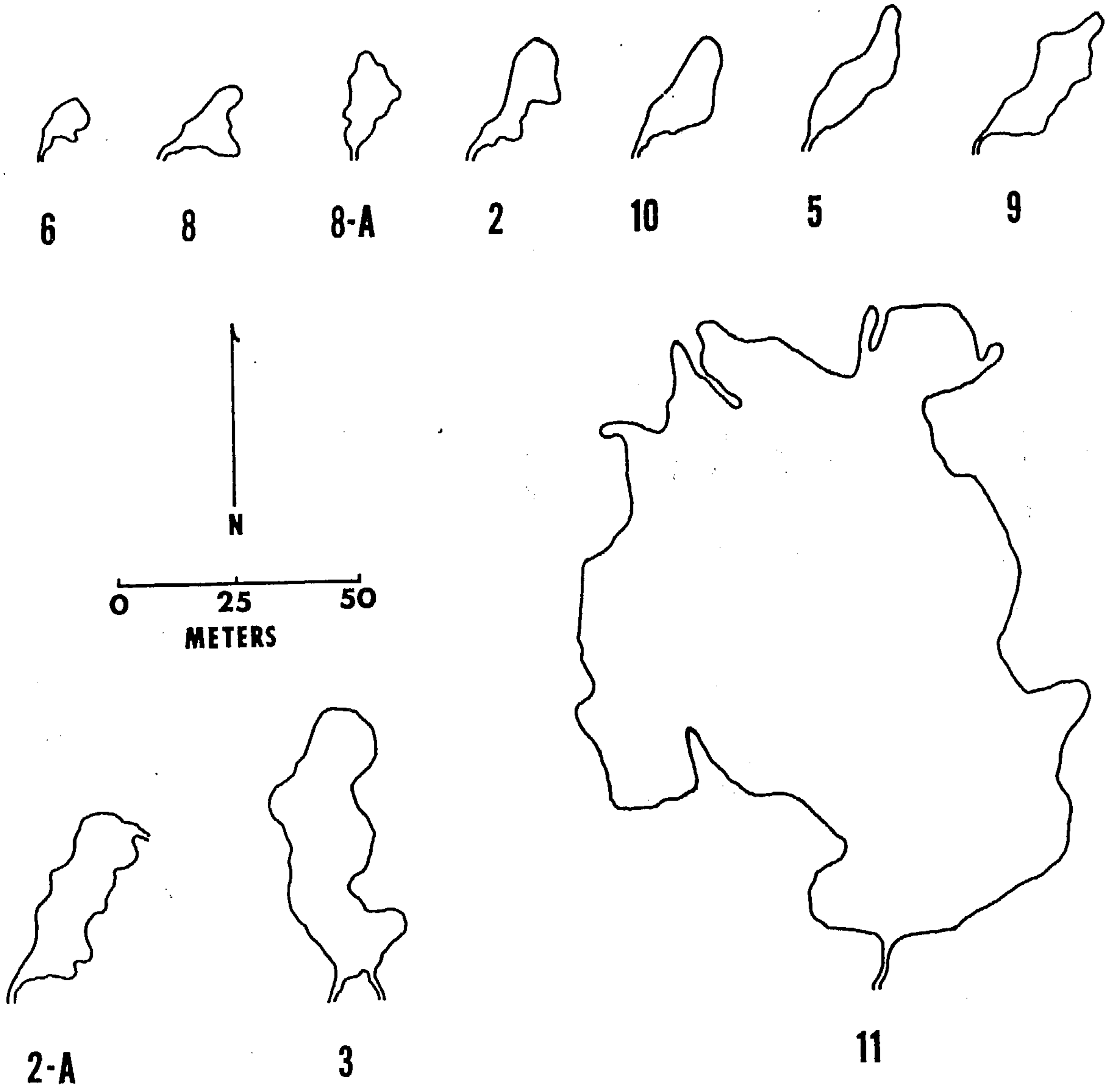

6
8
8-A
2
10
5
9
N
0
25
50
METERS
2-A
3
11

Table 1. Size of 11 marshes in the study area. See text for methods of determining areas of all except marsh 1, which was estimated.

Marsh No.	Area	
	m^2	Acres
11	8,744.9	2.161
3	750.6	0.185
2-A	394.4	0.097
9	233.6	0.058
5	185.8	0.046
10	172.4	0.043
2	157.3	0.039
8-A	117.5	0.029
8	104.0	0.026
1	101.6	0.020
6	55.8	0.014
Total Area	11,017.9	2.718

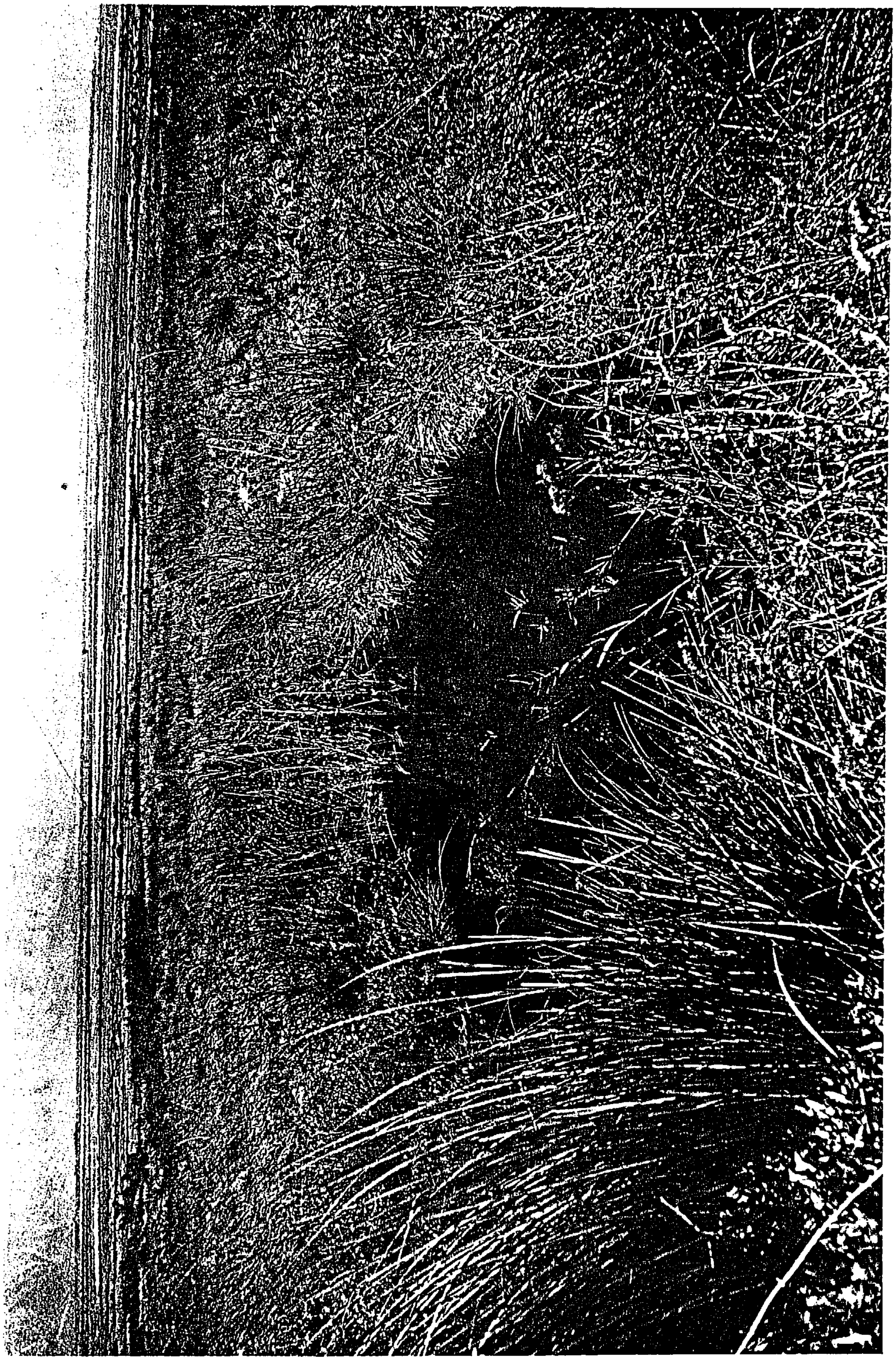
All marshes studied presumably receive their water directly or indirectly from a number of springs and narrow stream channels entering the area from the south, and all are oriented with their long axes generally from south to north (Fig. 7). The source of water for most of the marshes is subsurface springs leading to them by short surface drainage channels 10 to 20 m long. Water in these small streams is audible in its flow over marl bottoms in places. Often, the channels are well-covered by vegetation. Flow is north or northeast toward the Mojarral lagunas, a series of large ponds about a kilometer north of the study area. The channels tend to widen imperceptibly near a seep, or marsh, then become braided. Within a marsh, flow is re-reduced to trickles in many shallow (2 - 15 cm) rivulets. Substrate of the marshes is usually a dark mud. Less frequently, a lighter more calcareous, flocculent material is present. Most marshes have no visible water outlets, and evaporation and seepage apparently balance inflow. Two marshes (8-A and 3) have small, underground exit holes along their northeast borders, where water leaves in small streams about 10 cm wide and 2 - 5 cm deep. Underground stream courses are further evidenced by hollow-sounding regions and by several small (<50 cm diameter) sinkholes in the grassy terrain between marshes.

Three marshes in the study area receive their water directly from small, nearly circular, spring-fed ponds, or posas, approximately 4 to 6 m in diameter (Fig. 8). These connect with marshes 9, 3, and 11 by surface streams. These posas are about 7, 50, and 300 m from their respective marshes. The stream connecting marsh 11 with its posa disappears underground for a distance of about 75 m along its course. This channel is approximately a meter wide and carries the greatest volume of water of those observed in the study area.

Distances over dry land between adjacent marshes vary from 20 to 234 m (mean 125 m). No surface channels connect one marsh with another, with two exceptions. Marshes 8 and 8-A, about 20 m apart, have a common water source, the drainage channel dividing shortly before entering them. The surface exit channel from the north end of marsh 2-A nearly joins to marsh 2. The overland distance between these marshes is about 25 m. Webb et al. (1963:93) stated that "Most of the marshes are small and isolated, and some dry up in summer, often leaving deposits of salts." During July and August 1965 the surface water in several marshes in the study area evaporated during the day, exposing patches of wet mud, but water was always replenished overnight. No marsh in the study area was observed to desiccate completely.

Much of the study area, especially the intervening grass zones outside of the marshes, has been burned by man in recent years. Burned areas are locally extensive, but do not cover an area more than a few hundred square meters. Charred grass tussocks and young second-growth plants evidence

Figure 8. Posa, or small, spring-fed pool, in study area, 31 July 1965. Water temperature at all seasons averaged 33.5 C in this posa (no. 11).



old and recent fires over much of the area. Fires do not appear to kill larger shrubs, such as mesquite or acacia, and they do not seem to cause long-term damage to marsh vegetation. Sedges and other vegetation of large marsh areas in parts of the basin are sometimes destroyed by fires during winter when vegetation is dry, but there was no recent evidence that fire had entered any of the small marshes in the study area. Several box turtles were found with serious carapacial burn scars, and some mortality can probably be attributed to fires.

Herds of 5 to 15 semi-tame horses and mules traversed the study area almost daily during July and August 1965. These animals grazed almost exclusively in moist areas where succulent sedges and grasses were available, and frequently grazed within the marshes. _Eleocharis_ _rostellata_ seemed to be relished over most other kinds of plants, and the cover normally provided by this sedge to box turtles inhabiting the marshes was diminished. Seven of the ten smaller marshes had been severely grazed by horses. The _Eleocharis_ had been clipped to a height of approximately 10 to 20 cm over perhaps 80% of the surface of these marshes (Fig. 6). Horses usually avoided the muddy interiors of the larger marshes (3 and 11), often grazing the edges while standing on firm ground. Narrow, well-worn paths were between and around the edges. The only other livestock observed in the study area was an occasional transient herd of goats, but these usually did not remain longer than an hour, and caused no observable damage.

DESCRIPTION AND VARIATION

Color and Markings

Coloration and pattern of T. coahuila have been recorded by Schmidt and Owens (1944) and by Webb et al. (1963). The carapace has a uniform dark brown, brown, or olive-brown hue, which, in most specimens, is patterned with small, yellow, irregular lines, like worm tracks on the dark ground color. These markings were called "fine yellowish vermiculations" by Schmidt and Owens (1944:102). Not all T. coahuila possess such a vermiculated pattern. It is often difficult to see unless the carapace is dampened and inspected closely. Note was made, however, of its presence or absence in 106 adult or subadult individuals in the field; 71% showed some extent of pattern. Forty-eight preserved specimens were examined more critically in the laboratory and 77% possessed some pattern. Vermiculations may be sparse, or may cover most of the vertebral and upper portions of the costal scutes. Whether a turtle possesses or lacks these markings is seemingly not correlated with body size.

Although not related to color pattern, some specimens of T. coahuila have shallow radiating furrows in the carapace, particularly on the costal scutes. These furrows generally run down the sides (from the medial to peripheral border of the costal scutes, irregularly on the vertebrals), giving a slightly corrugated appearance to the carapace. No mention of such carapacial corrugations has been seen in the literature for any turtle, and their significance (in T. coahuila) is unknown.

The plastron of adults is plain dull yellow in color, but 13% of 48 preserved specimens had thin dark brown or black-rimmed sutures of the plastral scutes. More males (29%) than females (6%) showed development of dark pigment on the plastron, and it was present only in smaller specimens of both sexes.

The smallest available specimen of T. coahuila, a recently-hatched juvenile, caught 15 October 1966 (carapace 33.1, plastron 30.5 mm), has a carapace ground shade of olive-brown overlain by a mottled pattern of darker brown or black spots, most noticeable on the first vertebral and on the costal scutes. The marginals are lighter (dull brownish-yellow) with dark brown posterior borders. A prominent dorsal keel underlies the second, third, and fourth vertebral scutes. The plastron is a light grayish-yellow, except at sutures where there are thin dark lines. Wider dark areas are present at the interhumeral, interabdominal, and interfemoral sutures, and there is a dark blotch at the antero-medial corner of both anal scutes. Ventrally, the marginal scutes have the same ground hue as the plastron and also possess dark edges at sutures. Sides of the head are marked by a yellowish postocular stripe which widens to form a blotch. The antebrachial scales of the forelegs are light yellowish-gray, and the tail is marked by a distinct light stripe on the dorsal surface.

A juvenile collected and preserved on 20 August 1965 near the study area (carapace 51.4, plastron 49.8 mm) had solid yellow antebrachial scales on the forelegs, contrasting sharply with the dorsal brownish scales. A distinct, yellow, postocular stripe extended across the tympanum and graded into patches of brown, but continued posteriorly to the base of the skin fold of the neck. The throat was a marbled yellow as were the mandibular and maxillary beaks. The head was brown dorsally with a faint marbled pattern. Sides of the neck were predominately yellow, with a brown mottled pattern. Carapace markings consisted of short, dark, enlarged lines radiating from the central portion to the periphery of the first four vertebral and first three costal scutes. Both Cahn (1937) and Legler (1960) remarked that the carapace markings of _T. c. carolina_ and _T. o. ornata_, respectively, tend to radiate from the central portion of a scute as growth proceeds. Legler (1960:654) states: ". . . the radial pattern is generalized and primitive for _Terrapene_ . . . ." Webb et al. (1963:91) mentioned that juvenile _T. coahuila_ have ". . . more contrasting patterns on the carapace and head than do adults. The carapace has a fine, yellowish-buff and blackish marbled, or reticulated, or radiating pattern . . . ." These authors also noted the presence of a postorbital stripe in the smallest specimen they examined (plastron 47 mm).

Growth and Size

Reviews of the literature on growth in turtles were given by Cagle (1946) and Legler (1960), and they extensively analyzed growth in *Pseudemys scripta elegans* and *Terrapene o. ornata*, respectively. For terminology I have followed Legler (1960), and synonymous terms frequently used in growth studies are given in Table 2.

The usefulness of major growth-rings as indicators of growth and age depends upon four assumptions (Sexton, 1959a): (i) there is a discernible increase in growth each year; (ii) one major growth-ring is added per year; (iii) no major growth-rings are lost; and (iv) a major growth-ring of any selected scute does not change in length after its formation.

Legler (1960:568-569) states that growth of the epidermal laminae in *T. o. ornata* ". . . results from an entirely new laminal layer forming beneath, and projecting past the edges of the existing lamina" in the manner also described briefly by Carr (1952). Earlier, Ewing (1939) misinterpreted epidermal growth as occurring only at the margins rather than under the entire surface of the scute. Many authors have noted the presence of grooves, or growth-rings, on the epidermal laminae of the shells of turtles, and their apparent

Table 2. Terms used in growth studies of turtles.

Legler (1960)	Cagle (1946)	Sexton (1959a)	Ewing (1939
areola	birth plate	hatching annulus	———
annual growth zone	growth zone	primary annulus	annual growth zone
major growth ring	annulus	ridge	annual groove
minor growth ring	———	accessory annulus	pseudoannual growth zone

correlation with size and age (see citations in Cagle, 1946; also see Tinkle, 1958b; Sexton, 1959a). Minor growth-rings (as distinguished from major growth-rings) are caused by a temporary cessation of growth during unfavorable conditions in the course of the growing season, but ". . . do not result from the formation of a new layer of epidermis" (Legler, 1960:570). *T. o. ornata* frequently formed minor growth-rings, but these were shallower and less distinct than major growth-rings. Legler (1960:572) states: "Major growth-rings constitute a valuable and accurate history of growth that can be studied at any time in the life of the turtle if they have not been obliterated. They are accurate indicators of age only as long as regular growth continues . . ." (i.e., approximately up to the average time of attaining sexual maturity: 8 - 9 years in male, 10 - 11 years in female *T. o. ornata*).

Nichols (1939a) thought growth-rings in *T. c. carolina* formed regularly for the first 5 or 6 years, and that thereafter they gave no accurate indication of the number of growing seasons elapsed.

Some aquatic emydines tend to lose growth-rings through periodic shedding of the epidermal laminae (Sexton, 1965). In *P. s. elegans*, Cagle (1946) determined that growth-rings were reliable indicators of age only as long as an impression of the areola remained (up to 3 or 4 years, the time of attaining sexual maturity). Growth-rings in *C. p.*

marginata began to disappear after about 5 to 7 growing seasons, and minor growth-rings ("accessory annuli") were formed in some juvenile Chrysemys at shedding (Sexton, 1959a).

By comparing the medial length of the first growth-ring on the plastral scutes of juvenile P. s. elegans and C. picta after several growing seasons, with the plastral lengths of hatchlings, Cagle (1946, 1954) concluded that growth-rings remain the same size once they are formed. Sexton (1959a) confirmed this, noting that growth-ring lengths stayed unchanged on successive captures of marked C. p. marginata. Legler (1960) compared five groups of T. o. ornata (hatchlings, juveniles, subadults, adult males, and adult females) with respect to the length of the abdominal scute as a percentage of the plastron length, but discerned no significant differences, showing a constant proportion between these two variables throughout life. A formula by Cagle (1946 - from Sergeev, 1937 - where the present length of the scute is to the present length of the plastron as the length of any growth-ring on the scute is to the former length of the plastron at the time that growth-ring was formed) was utilized by Legler (1960) to estimate plastral lengths of T. o. ornata at any previous age from measurements of growth-rings on the right abdominal scute.

It was, unfortunately, not possible to estimate growth and age in T. coahuila using growth-rings, except in a few small specimens. Growth-rings are obscured after several years, presumably by wear, as no turtles were found to be shedding their epidermal scutes, so that nearly all subadult and adult turtles have a completely smooth carapace and plastron, or, at best, exhibit only traces of a few recently-formed growth-rings on the abdominal or pectoral scutes of the plastron. Other methods of aging, such as a possible correlation between the number of rings in limb bones with body size, as reported by Mattox (1936) for C. picta, were not attempted.

Four juveniles, three collected in or near the study area and one (shell only) from an unknown locality in the basin, provide some data on approximate size at hatching and early growth, since growth-rings are still evident. Growth-rings were measured to the nearest tenth of a millimeter on the medial side of the right abdominal scute in the manner described by Sexton (1959a) and Legler (1960). Sergeev's proportion was used to calculate previous plastral lengths.

Plastron lengths at hatching are estimated at 26.1 and 29.0 mm in two juveniles (Table 3). Sizes at hatching for 17 T. c. carolina are comparable, ranging from 26 to 30, mean 28.1 mm (Allard, 1948). Babcock (1939), Myers (1952), and Crooks and Smith (1958) reported similar hatching sizes in T. c. triunguis. The smallest T. coahuila known may be one to three months old as interpreted from its growth increment (17% of the plastron length at hatching) and judging

Table 3. Size and age of four juvenile *Terrapene coahuila* as determined from growth-rings. Probable dates of hatching and dates of collection are indicated in parentheses; measurements in milimeters.

Estimated plastron length at hatching	Plastron length at first winter	Plastron length at second winter	Plastron length up to time of capture	Estimated age
26.1 (July - Sept. 1966)	——	——	30.5 (15 Oct. 1966)	1 - 3 mos.
29.0	36.3	43.6	49.0	2 years
? (Sept. 1963)	36.4	54.2	57.1 (15 July 1965)	1 year 10 mos.
? (Sept. 1963)	?	?	49.8 (20 Aug. 1965)	1 year 11 mos.

from the probable season of hatching in the population (mid-July to December). September is a likely month of hatching for two other juveniles (Table 3), since it holds a roughly median position in the hatching season. Legler (1960) recorded a 17.5% increment in plastron lengths of those T. o. ornata which grew in the season of hatching, a 68.1% increase in the season following hatching, and decreasing each year thereafter (28.6% in the second season, 18.1% in the third, etc.) Since hatchling T. coahuila can emerge earlier from the nest and remain active longer than more northern species of Terrapene, growth in the season of hatching may be considerable. One juvenile increased an estimated 25% of its original plastron length in the season of its hatching. Calculated increases of 20% and 49% of estimated plastron lengths at the end of the hatching season were made by two juveniles in their first full season of growth (Table 3).

Mosimann (1956), in a study of plastral scute midline variation of Kinosternon integrum, has shown that the ratio formula (implying a lack of differential growth between the scute length concerned and plastron length) can substitute for regression analysis when scute length (abdominal) is used as the independent variable and plastron length is estimated from the regression line. He accurately estimated past plastral sizes from the plastron length on abdominal scute length regression, despite a very slight relative increase in the latter. Using this regression for 48 preserved specimens of *T. coahuila*, six past plastral sizes calculated for three juveniles ranged from 12.3 to 19.0 mm greater than plastron lengths derived from Sergeev's formula. A proportional increase of the abdominal scute length to plastron length (Y on X regression) would reduce the regression coefficient in the converse relationship (X on Y regression), thus making the relationship between these two variables over the size range utilized (plastron lengths 80.3 - 137.8 mm) unsuitable at smaller plastral lengths.

Carapace lengths in the *T. coahuila* population studied are notably smaller than *T. carolina*, *T. ornata*, and *T. nelsoni*. Males from the study area averaged 108.9 mm in carapace length (n = 70) and females averaged 100.9 mm (n = 94). Nichols (1939a) gives size distributions of 387 *T. c. carolina* from New York in which most females were about 133 mm and most males about 140 mm in plastron length. *T. c. carolina* in Maryland over 118 mm in carapace length had well-developed secondary sex characters and were considered mature by Stickel (1950). Other subspecies of *T. carolina* (*bauri*, *major*, *triunguis*) in southeastern USA (Carr, 1952; Auffenberg, 1958; Milstead, 1967), *T. o. ornata* in Kansas (Legler, 1960), and *T. n. nelsoni* in western Mexico (Milstead and Tinkle, 1967) surpass greatest sizes attained by nearly all female and most male *T. coahuila* in the population from the study area. However, *T. coahuila* elsewhere in the basin are larger. Mean plastron length of 26 adults (8 males, 18 females: 12 preserved, KU collection; 14 living, ASU collection) from scattered localities in the basin is 122.3 mm (range 100.1 - 153.2 mm), and mean carapace length of 10 adults (four males, six females) from Posas de la Becerra was 121.5 mm (range 103.0 - 153.0 mm). Thirteen T. coahuila (including the type specimen) measured by Schmidt and Owens (1944) ranged from 135 to 155 mm in carapace length. Webb et al. (1963) give 164 mm for males and 159 mm for females as maximum sizes, and Milstead (1967:177) states: "The maximum size of coahuila is not as great as that of major or putnami, but it is greater than in most living box turtles."

Sexual Dimorphism

Some important differences between sexes of box turtles are the following: (i) posterior lobe of plastron concave in males (more pronounced in the Carolina group than in the Ornata group), flat or slightly convex in females (Cahn, 1937; Nichols, 1939a; Evans, 1952; Legler, 1960; Milstead and Tinkle, 1967); (ii) iris of eye in T. c. carolina and T. o. ornata reddish colored in males, brownish in females (Cahn, 1937; Nichols, 1940; Evans, 1952; Legler, 1960); and (iii) larger, more abruptly curved rear claws of male T. c. carolina (Cahn, 1937; Evans, 1951, 1952) and first toe of hind foot turned inward in male T. ornata and T. nelsoni, but not so modified in the Carolina group or in females of the Ornata group (Legler, 1960; Milstead and Tinkle, 1967). Other differences that have been noted are a longer precloacal distance of the tail (Cahn, 1937; Carr, 1952) and more flared posterior marginal scutes (Cahn, 1937; Milstead and Tinkle, 1967) in males. A longer precloacal distance and generally larger tail are particularly evident in male kinosternids and chelydrids (Risley, 1930; Tinkle, 1958b; Mosimann and Bider, 1960; Sexton, 1960) and in males of many emydines (Cagle, 1948, 1954; Carr, 1952; Barton and Price, 1955).

Schmidt and Owens (1944) stressed difference in plastral indentation between male and female _T. coahuila_, and, along with Webb et al. (1963), noted a more prominently notched maxillary beak in males. Color or pattern differences are lacking: males were not distinguishable from females on this basis in the field during my study. More flared marginals were present in some large males, and males often appeared flatter than females. The concave plastron of males was the most useful field character for sex determination, but it was frequently necessary to confirm the sex by inspecting the somewhat more bulky tail of males and the more spacious cloacal cavity of females. External traits that best distinguish the sexes in _T. coahuila_ are as follows:

	males	females
1.	Posterior lobe of plastron indented (concave).	Posterior lobe of plastron flat or convex.
2.	Tail longer, thicker at base.	Tail shorter, thinner at base.
3.	Carapace relatively lower (average height/length ratio about 43%).	Carapace relatively higher (average height/length ratio about 46%).
4.	Iris brownish, flecked with yellow.	Iris yellowish, flecked with brown.

To study sexual dimorphism in morphological characters involving the shell, the following measurements were taken to the nearest tenth of a millimeter in 164 adult or subadult *T. coahuila* in the field: *carapace length* (CL), the median straight-line distance (not along the curve of the back) from the most anterior to the most posterior part; *carapace height* (CH), the maximum straight-line height of the shell, measured as perpendicular to the plastron opposite the bridge; *carapace width at bridge* (BR-W), the straight-line width of the carapace across the anterior portion of the bridge at the hinge (or, at about the contact between the fifth and sixth marginal scutes); *posterior carapace width* (POST-CW), the maximum straight-line width of the carapace at the widest point, usually at the eighth or ninth marginal scute; *plastron length* (PL), the median length of the plastron along a straight line; *anterior lobe of plastron length* (ANT-L), the mid-line length of the first three plastral scute pairs anterior to the hinge between pectoral and abdominal scutes; posterior lobe of plastron length (POST-L), the mid-line length of the last three plastral scute pairs posterior to the hinge. Because all Coahuilan box turtles closed their shells tightly when handled, it was necessary to measure the anterior and posterior plastral lobes separately and to express total plastron length as the sum of these two components.

Six bi-variate relations between the above measures were developed (Table 4; Figs. 9 - 14). Statistical methods and analysis are based mainly on the studies of Mosimann (1956; 1958a) and Mosimann and Bider (1960), who have pointed out that since there is no true independent (or fixed) variable in any of the cases as used here where regressions are run on body measurements of the same growing animal, the applications of regression are not strictly valid. These authors employed both X on Y and Y on X regressions (assuming each variable in turn as independent) to predict the value of one variable from another. Neither regression can give a single estimate of the joint relation between X and Y, but when high correlations exist, and "Since the Y on X and the X on Y lines are the same when r is unity, there is little difference between the regressions or interpretations from them where computed from either Y or X deviations" (Mosimann, 1958a:157-158). Correlation coefficients in all relations studied in T. coahuila are high, ranging from 0.82 to 0.99. I was primarily interested in determining if males

Table 4. Statistical data and regressions of linear relations for carapace and plastron measures (see text for abbreviations) in *Terrapene coahuila*. Symbols used: n = sample size; $\overline{x}$ = mean of X values; $\overline{y}$ = mean of Y values; r = correlation coefficient; a = Y intercent value; b = regression coefficient; s^2_{YX} = sample variance from regression.

Variables Related	Sex	n	$\overline{x}$	$\overline{y}$	r	Y = a + bX	s^2_{YX}
BR-W (Y) vs CL (X)	M	70	108.88	69.88	.931	Y = 10.65 + 0.544 X	3.91
	F	94	100.93	65.76	.876	Y = 10.75 + 0.545 X	2.88
POST-CW (Y) vs CL (X)	M	70	108.88	73.94	.946	Y = 8.61 + 0.600 X	3.69
	F	94	100.93	69.27	.883	Y = 7.60 + 0.611 X	3.37
CH (Y) vs CL (X)	M	70	108.88	46.69	.874	Y = 12.94 + 0.310 X	2.57
	F	94	100.93	46.06	.815	Y = 10.33 + 0.354 X	2.03
ANT-L (Y) vs PL (X)	M	63	106.74	40.09	.967	Y = - 0.47 + 0.379 X	0.71
	F	93	100.31	37.49	.927	Y = - 1.83 + 0.392 X	0.75
POST-L (Y) vs PL (X)	M	63	106.74	66.65	.987	Y = 0.37 + 0.621 X	0.71
	F	93	100.31	62.82	.966	Y = 2.43 + 0.602 X	0.76
PL (Y) vs CL (X)	M	63	108.90	106.74	.978	Y = 13.09 + 0.860 X	3.13
	F	93	100.87	100.31	.961	Y = 7.11 + 0.924 X	2.27

differ from females in relative shell dimensions, so only the Y on X regression was calculated. Best-fitting regression lines were calculated by the method of least squares. In all relations, CL and PL were used as the independent variables; in the relation PL/CL, carapace length was the independent variable. Only closely associated parts were related, such as CH vs CL, or POST-L vs PL. Mosimann (1956: 38) states: ". . . it is desirable, for understanding or for attempting to understand what the variability of a ratio expresses, to compare parts which can be biologically closely connected; for example, a plastral scute with plastron length."

Males and females are nearly identical in BR-W/CL (Fig. 9), POST-CW/CL (Fig. 10), ANT-L/PL (Fig. 11), and POST-L/PL (Fig. 12). In all these relations, males show higher r values (Table 4) and a corresponding greater proportion of the variation in Y, as measured by sum of squares, due to linear regression of Y on X. Slight sexual dimorphism is seen in the PL vs CL regression (Fig. 13), with the plastron length of females increasing relatively faster than that of males as carapace length increases. The difference between the regression coefficients was not significant, however ($t = 1.73$, $P > 0.05$). This sexual difference also was observed, and the variables plotted, in Kinosternon integrum (Mosimann, 1956), Sternothaerus odoratus (Risley, 1930), and several other species of Sternothaerus (Tinkle, 1958b).

Figure 9. Relationship between carapace width at bridge (BR - W) and carapace length (CL) in 160 *T. coahuila* (66 males, 94 females) from study area.

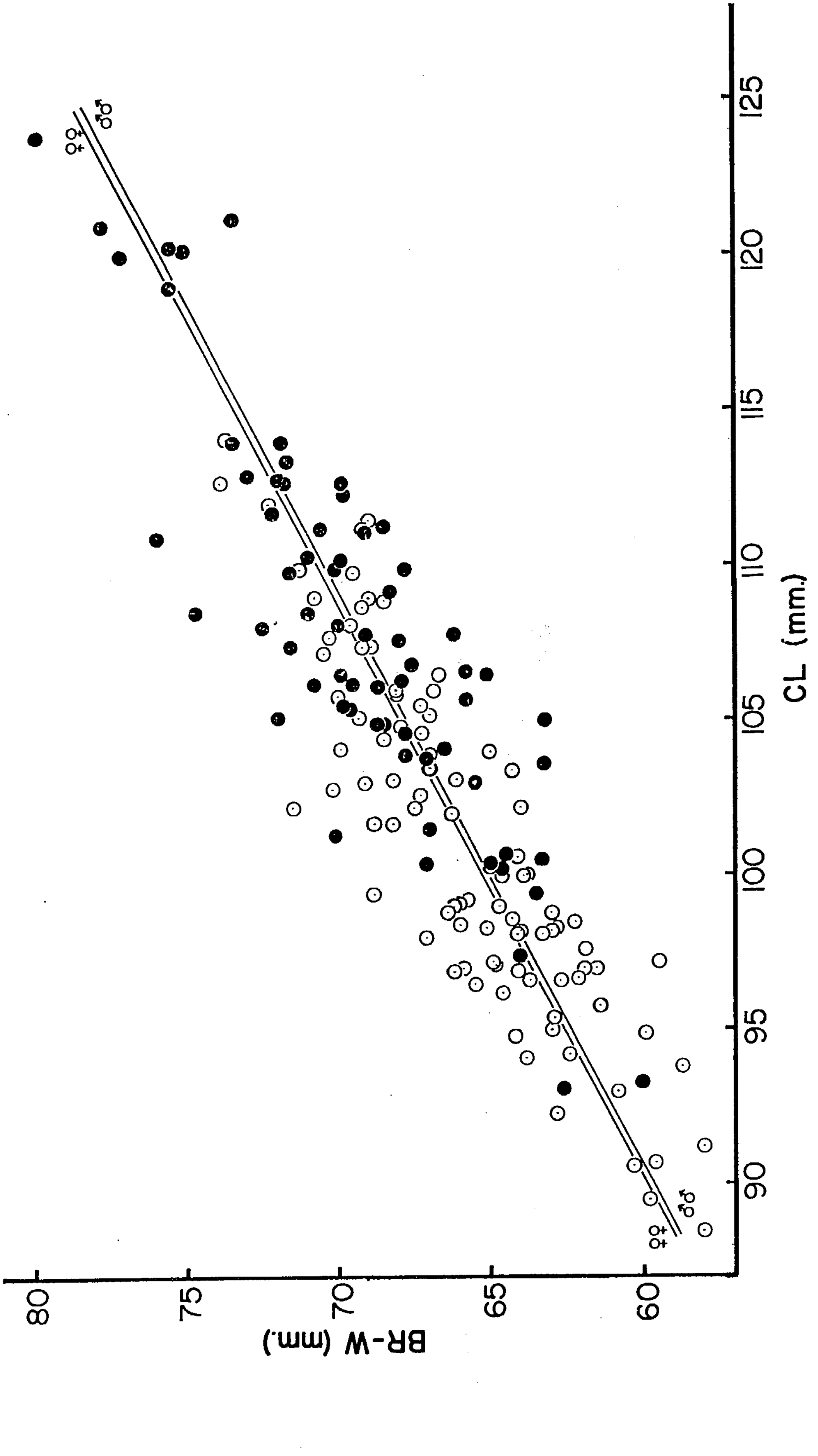

BR-W (mm.)
60
65
70
75
80
CL (mm.)
90
95
100
105
110
115
120
125
♀♀
♂♂
♀♀
♂♂

Figure 10. Relationship between posterior carapace width (POST - CW) and carapace length (CL) in 159 *T. coahuila* (65 males, 94 females) from study area.

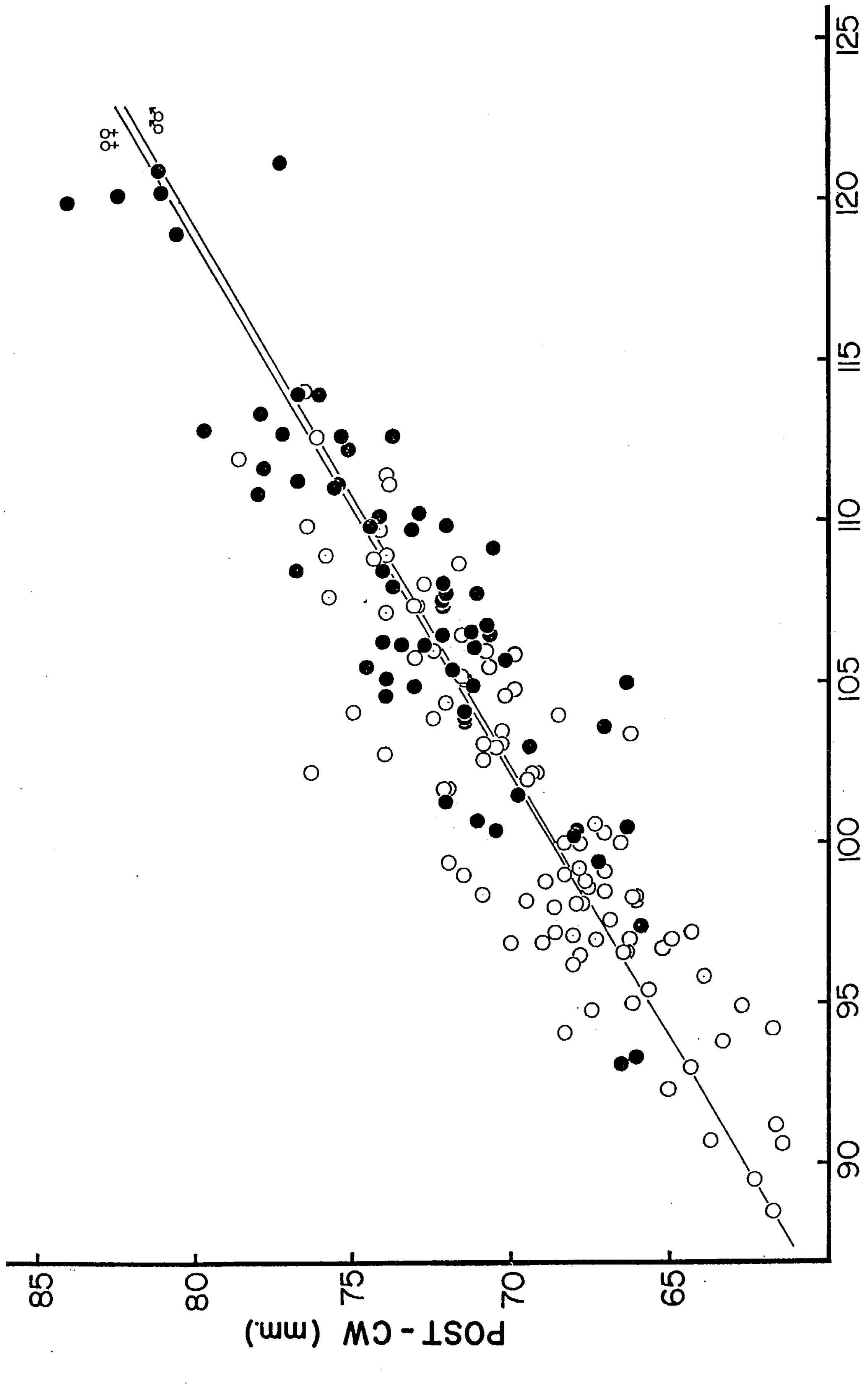
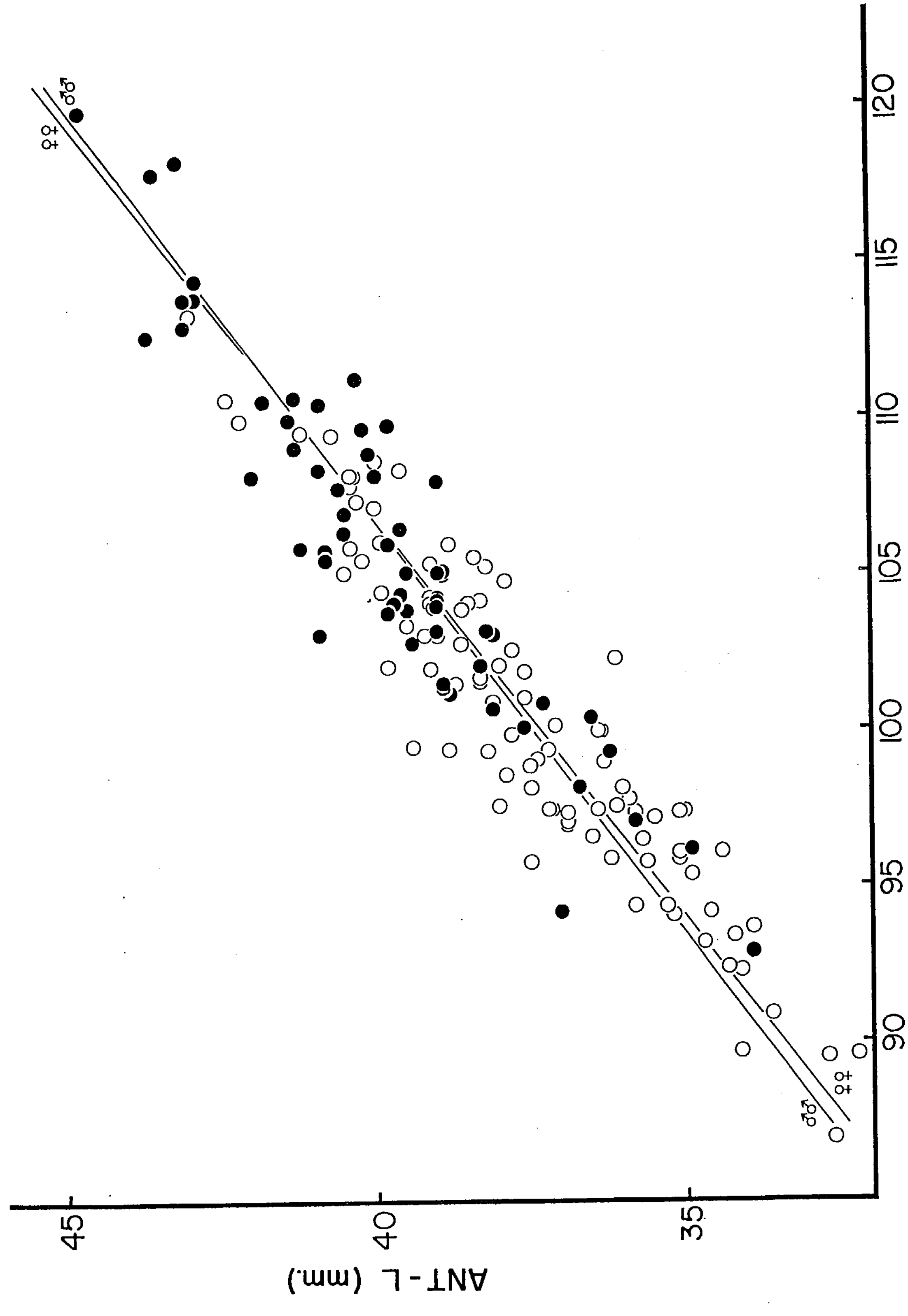

♀♀
♂♂
CL (mm.)
90
95
100
105
110
115
120
125
POST - CW (mm.)
65
70
75
80
85

Figure 11. Relationship between anterior lobe of plastron length (POST - L) and plastron length (PL) in 152 *T. coahuila* (59 males, 93 females) from study area.



ANT-L (mm.)
45
40
35
PL (mm.)
90
95
100
105
110
115
120
♀♀
♂♂
♀♀
♂♂

Figure 12. Relationship between posterior lobe of plastron length (POST - L) and plastron length (PL) in 152 T. *coahuila* (59 males, 93 females) from study area.

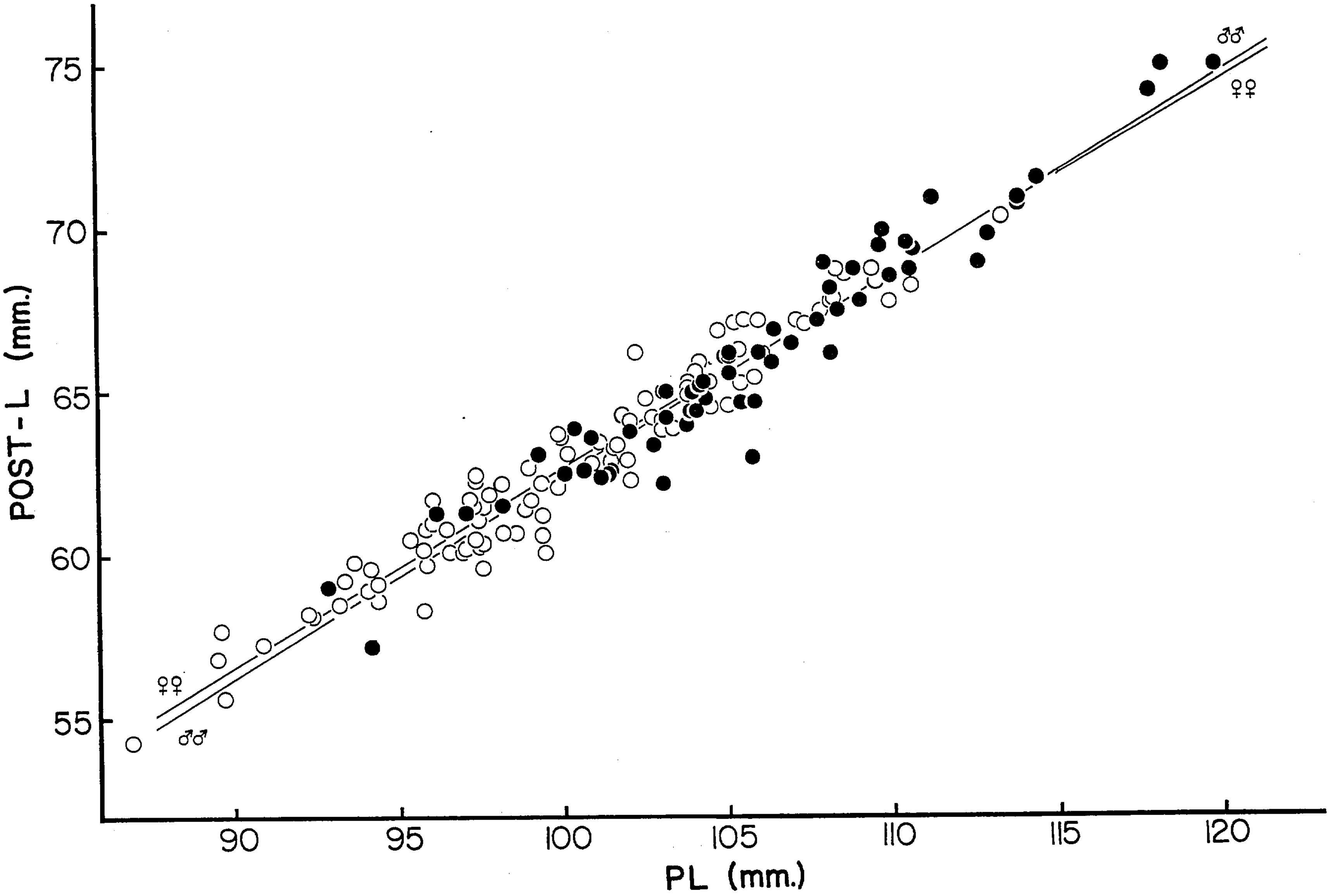

♂♂
♀♀
♀♀
♂♂
75
70
65
60
55
90
95
100
105
110
115
120
POST-L (mm.)
PL (mm.)

Figure 13. Relationship between plastron length (PL) and carapace length (CL) in 152 *T. coahuila* (59 males, 93 females) from study area.

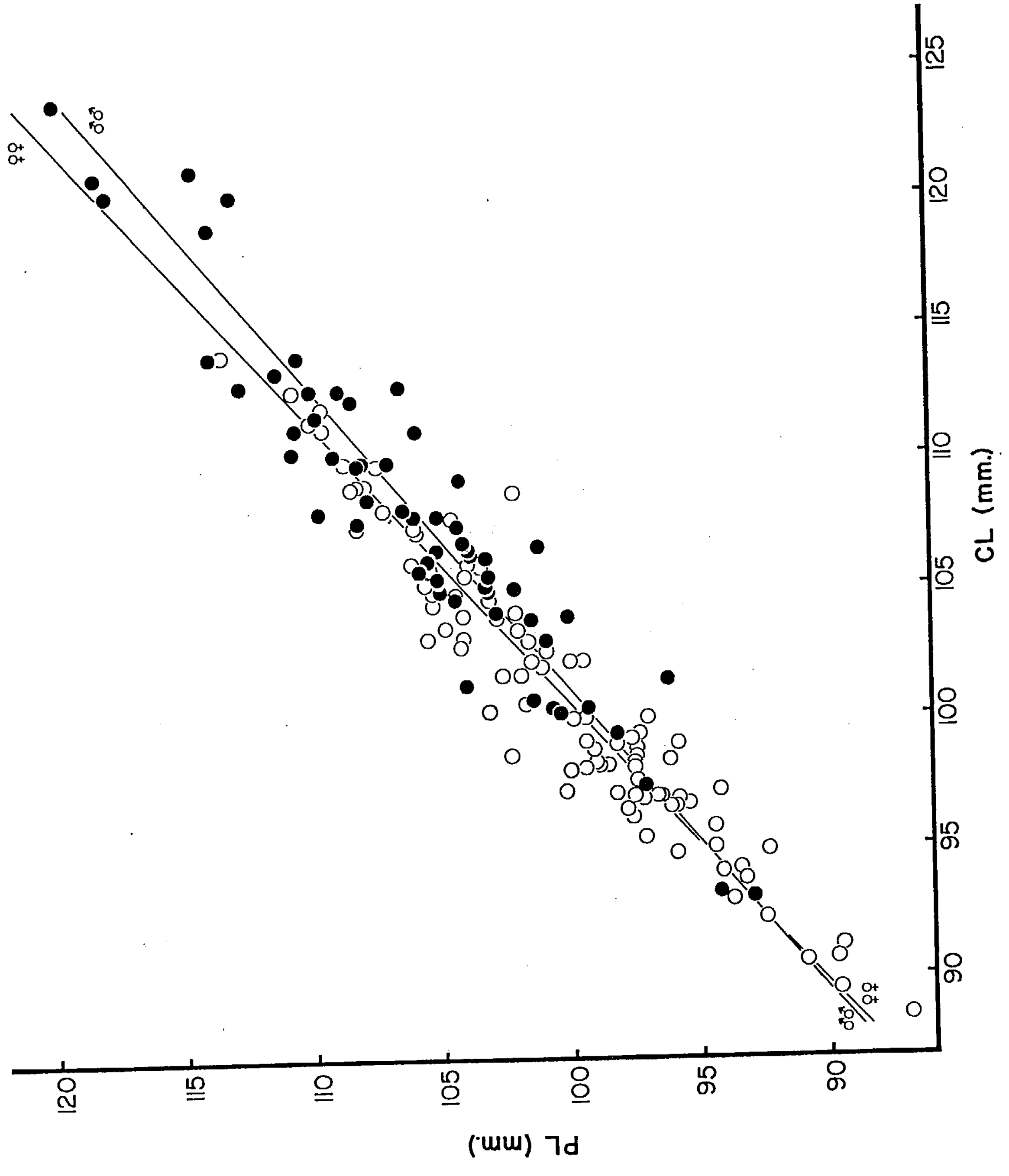
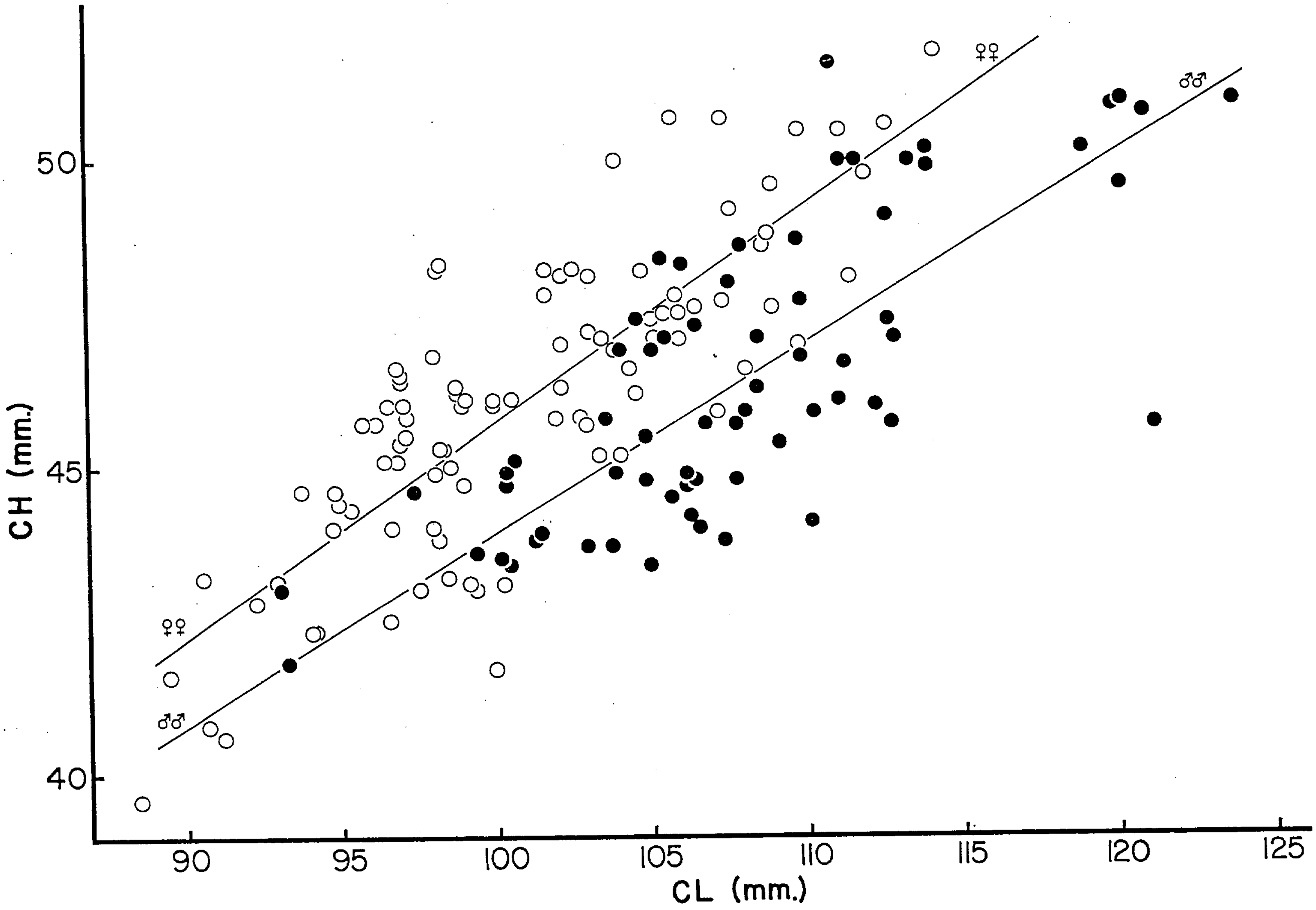

PL (mm.)
120
115
110
105
100
95
90
CL (mm.)
90
95
100
105
110
115
120
125
♀♀
♂♂
♂♂
♀♀

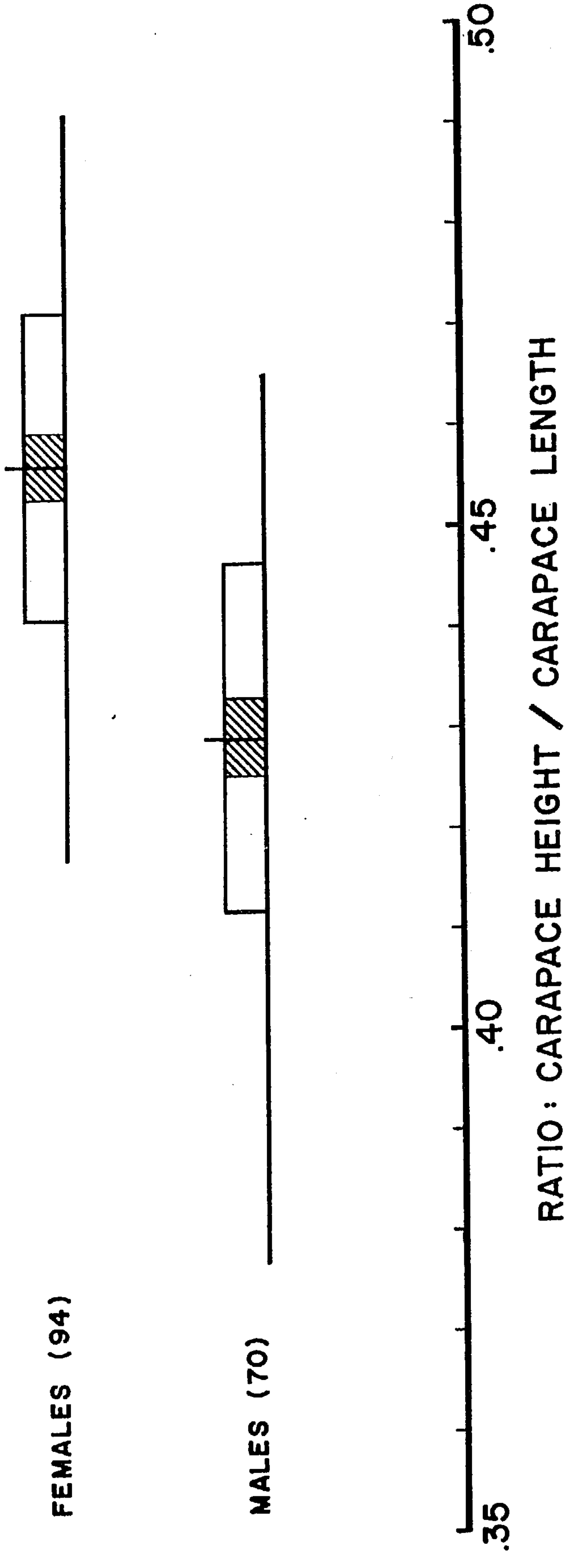
Figure 14. Relationship between carapace height (CH) and carapace length (CL) in 160 *T. coahuila* (66 males, 94 females) from study area.


♀♀
♂♂
♀♀
♂♂
CH (mm.)
50
45
40
90
95
100
105
110
115
120
125
CL (mm.)

Legler (1960) observed that 30% more adult female than male T. o. ornata had plastrons longer than carapaces, suggesting a similar relationship.

Although the regression coefficients do not differ significantly ($t = 1.29$, $P > 0.10$), the relationship showing strongest sexual difference in T. coahuila is CH/CL (Fig. 14). Schmidt and Owens (1944:102) alluded to this difference when they described a female as having the shell ". . . a little more arched in lateral outline. . . ." In 70 males over the size range studied (carapace length 81.9 - 143.5 mm), carapace height ranged from 37.7 to 46.5% of carapace length, mean 42.9%; in 94 females (carapace length 88.5 - 114.1 mm) carapace height ranged from 41.7 to 49.1% of carapace length, mean 45.6%. The CH/CL ratio is significantly higher ($P < 0.01$) in females than in males (Fig. 15). Chrysemys picta marginata females are relatively higher than males (Mosimann, 1958a), and Legler (1960) reported that female T. o. ornata are relatively higher (height/length 50 - 69%) than males (height/length 44 - 60%). Barton and Price (1955) also found the ratio of height to length in female Clemmys muhlenbergi to be significantly greater than that of males, but did not calculate a regression of the original measurements. Marr (1955) has urged the use of regression methods rather than analysis of ratios, stating (p. 29-30): ". . . ratios, averages of ratios, or regressions of ratios . . . as opposed to the regression analysis of original variates, are inefficient

Figure 15. Sexual dimorphism in ratio of carapace height to carapace length in 164 adult *T. coahuila*. Horizontal and vertical lines show range of variation and mean, respectively; solid and open blocks represent 95% confidence limits and one standard deviation, respectively, on each side of the mean.


FEMALES (94)
MALES (70)
.35
.40
.45
.50
RATIO : CARAPACE HEIGHT / CARAPACE LENGTH

and may often lead to erroneous interpretation." Mosimann (1958a:149) agreed, stating that: ". . . regression analysis of original data is often superior to that of ratios." In this sense, it is interesting that the regression analysis shown here for T. coahuila (Fig. 14) indicates that females are relatively (but not significantly) higher than males, whereas reliance on the ratio plots alone (Fig. 15) tends to overstate the difference. In addition, a ratio provides no way to estimate the value of one variable from the known value of another as can easily be done using a least squares linear regression equation.

Scute Abnormalities

Of 218 Coahuilan box turtles examined (169 alive in the field, 49 preserved, 11 (5%) had either extra epidermal ("supernumerary") scutes or had less than the normal number, and five had incomplete or abnormal (usually crooked) interlaminal sutures. All scute anomalies occurred on the carapace, but distorted sutures were present on both carapace and plastron. Reduction of the normal number of all three series of carapace scutes was observed in four individuals, as follows: three costals on both sides; three costals and 11 marginals on both sides; four vertebrals; 11 marginals on both sides; and 11 marginals on right side only. Seven individuals possessed one additional scute (either seemingly inserted between existing normally-shaped scutes, or added by a mid-line suture in an existing normally-shaped scute) as follows: six vertebrals formed by a small accessory scute between the second and third vertebrals (two turtles); six vertebrals formed by a mid-line division of the second vertebral (three turtles); five right costals formed by a divided (Y-shaped) first intercostal suture near the fifth marginal; and five right costals formed by a median suture in the first costal.

Scute anomalies have been observed in T. c. carolina by Knoll (1935) and Lynn (1937). Milstead (1956:167) observed that ". . . such anomalies as a fifth costal or a sixth vertebral scute are not uncommon in T. carolina . . . ." Cagle (1950) recorded carapace scute abnormalities in 5.7% of 860 Pseudemys scripta elegans from Illinois. Coker (1910), Lynn (1937), and Carr (1952) have reviewed and discussed the considerable number of earlier publications on the subject, which dealt mostly with the phylogenetic significance of laminal variation. Perhaps the most significant recent approach is the experimental work of Lynn and Ullrich (1950) who demonstrated that scute abnormalities can be produced by partial desiccation of the egg during development.

REPRODUCTION

Methods

Reproductive systems of 48 preserved _T. coahuila_ were examined. The turtles were opened by sawing through the left bridge; the plastron could then be laid to one side after it was freed of muscles and connective tissue joining it to the limb girdles. Measurements and weights of the various reproductive structures were determined immediately after removal.

Measurements and weights of testes from male _T. coahuila_ were determined with vernier calipers and a triple-beam balance. Volumes of testes were estimated to the nearest tenth of a milliliter by water displacement in a graduated cylinder. Epididymal smears were obtained from each male and examined under a compound microscope for the presence of sperm. Several smears also were made from macerated testes and examined for sperm.

Ovaries and oviducts of 34 female _T. coahuila_ were removed and ovarian follicles, corpora lutea, and oviducal eggs were counted. Follicles greater than 1 mm in diameter were measured with vernier calipers to the nearest millimeter. Eggs were measured to the nearest tenth of a millimeter. Ovaries and eggs were weighed to the nearest hundredth of a gram with a triple-beam balance after being trimmed of superficial connective tissue and blotted with an absorbent paper towel to remove excess fluid. The condition and relative size of the oviducts were noted and each ovary was kept with its corresponding oviduct of the same side. No allowance was made for possible shrinkage through preservation. Legler (1960) noted that preserved ovaries of _T. o. ornata_ were 13% lighter than fresh gonads.

Mating

Coahuilan box turtles have been observed to mate under semi-natural conditions in an artificial outdoor pond at Tempe, Arizona. The pond is roughly circular, about 8 x 10 m. About half of its area is shallow (ca. 1 - 20 cm), and half deep (ca. 1.0 m). In April 1966 I observed a male mounted on a female in relatively deep (ca. 25 cm) water in this pond. The male's rear claws gripped the posterior of the female, apparently on the skin of the gluteal region or on the plastron, and he snapped at the female's head. The female was completely submerged, making violent attempts to climb out of the water, which she could not do because of the slippery inclined bottom. After about 15 minutes, she succeeded and the pair separated. Whether intromission had occurred is not known.

Copulations were observed in the artificial pond on 10 dates between 16 September 1965 and 11 June 1966 by W. L. Minckley (unpublished data). No matings were recorded in October, January, and February. Most pairs were in shallow water and in all cases males were lying on their backs. On

1 November 1965 a male in shallow water "butted the female's shell twice" (presumably with his shell) before mounting the submerged female. On 23 March 1966 at 7:40 AM a male was following a female with head extended, pushing the back of the female's carapace. The male then retracted his head and "bumped the female with his carapace." Two hours later these individuals were found in copulation. The first of three phases of mating in T. c. carolina discerned by Evans (1953) consisted of the male pushing, circling, and biting at the female's carapace and striking it with the anterior portion of his plastron. Brumwell (1940) saw a male T. o. ornata striking the carapace of a female with his plastron and biting at her carapace before mounting.

Minckley (unpublished data) observed 2 different copulating pairs of T. coahuila on 4 March 1966 at 7:40 AM, and three pairs on the morning of 17 March 1966. Twice, a male's hind legs were observed to be clasped by the female. Cahn and Conder (1932) described copulation in a pair of captive T. c. carolina in which the hind legs of the male were inserted between the plastron and carapace of the female and were held tightly in place by the hind legs of the female. The male fell backward to lie on his carapace during copulation. Evans (1953) noted that copulation occurred in T. c. carolina when the male slid backward and was held by the hind legs of the female outside of and pressed against the male's. The modified first claw of the hind feet of male T. o. ornata ordinarily grip the skin under the female's legs while the other three claws grip the edge of the plastron (Legler, 1960). Secured by the hind legs of the female, the male falls backward and effects coitus. Legler (1960) states that the coital position of T. carolina differs from that of T. ornata in the position of the male's legs. It seems necessary for male box turtles to tilt backward to achieve effective copulation, perhaps because of their relatively short tails and highly-domed shells. Minckley recorded copulation times in two observations of T. coahuila of approximately two hours, and two hours and twenty minutes. Evans (1953) stated that the entire courtship of T. c. carolina lasted up to six hours with up to two hours in copulation. Brumwell (1940) recorded a 30-minute copulation time in T. o. ornata.

Copulating pairs of Coahuilan box turtles were found three times under natural conditions. Minckley (unpublished data) discovered a copulating pair of T. coahuila in early April 1963 at Rancho de San Marcos, about 20 km southwest of Cuatro Ciénegas. The turtles were in water about 2 cm deep in a small pond. On 31 December 1964, at approximately 12:00 noon, a pair was discovered at the edge of dense growth of Baccharis along the edge of a marsh in my study area. The substrate was soft and muddy, with shallow water nearby but not directly under the turtles. The weather was slightly overcast, air temperature 26.7 C. Temperature of the mud directly beneath the turtles was 17.2 C. The female was partially hidden by overhanging vegetation and the male lay on his carapace. When disturbed, cloacal contact was broken and both individuals withdrew into their shells, remaining in their original location. Two other turtles, a male and a female, were found 1 m and 3 m, respectively, from the copulating pair.

A third instance of copulation was recorded on 8 April 1966 at 4:30 PM in marsh 5. The central and eastern parts of the basin had received light rain two hours earlier, but the study area received only a trace. Otherwise, the weather was clear and humid, air temperature 29.0 C. Temperature of water near the marsh inlet was 22.6 C. Both turtles were in shallow water (2 - 5 cm). The male was lying on his carapace and was being dragged slowly by the female. They soon separated, and both began to burrow rapidly into the mud. Three other turtles were foraging within 5 m of the copulating pair. Two of these turtles, a male and a female, were examined; the third escaped.

Legler, in Webb et al. (1963), noted that a female was drowned by a male during mating in an aquarium. Mating in the marshes of my study area could rarely occur in water deep enough to drown a female, but in other habitats (posas; pools of the Río Mesquites) the water is deep enough so that this might conceivably occur, but very few turtles were ever seen in posas in the study area, and no matings were noted while observing turtles on several occasions in pools along the river.

Mating in *T. carolina* and *T. ornata* occurs in the spring after emergence from hibernation (Ewing, 1933; Allard, 1935) and less frequently in the fall prior to hibernation (Ewing, 1935; Allard, 1935; Rosenberger, 1936). It is reported sporadically throughout the season of activity, approximately from April to October at Washington, D.C., for *T. c. carolina* (Allard, 1935, 1949), and from mid-April to late October for *T. o. ornata* in Kansas (Legler, 1960). Penn and Pottharst (1940) observed that mating in *T. c. major* at New Orleans, Louisiana, was coincident with favorable temperature and relative humidity. Most matings occurred after a rain or when temperatures were between 21.1 and 26.7 C. Twice, mating occurred in water.

The record of December mating by *T. coahuila* substantiates data for year-round activity of at least part of the population. Whether mating occurs sporadically throughout the year is not known, but from observations of captive and of wild turtles, it occurs frequently from September to June and is most concentrated in March and April. No matings were observed during July and August 1965, the period of most intense field work.

Sexual Maturity and Seasonal Cycle - Males

Criteria for sexual maturity in male turtles are:

enlarged testes; enlarged epididymides; enlarged and convoluted vasa deferentia; and the presence of sperm in the testes, epididymides, or vasa deferentia (Cagle, 1948; Tinkle, 1961). Male T. coahuila were considered to be sexually mature if sperm were present in the epididymides.

Ten of 14 males dissected had sperm in the epididymides. Mean carapace length of these was 109.5 ± 2.2 mm. Based on this sample, 95% of mature males in samples from the study area would be expected to fall between 104.6 and 114.4 mm. The smallest mature male was 93.1 mm. The smallest mature male of T. o. ornata reported by Legler (1960) had a plastral length of 99 mm; 76% of the males were mature at plastral lengths of 100 to 109 mm, and all were mature between 110 and 119 mm (in T. o. ornata plastral lengths are shorter than carapace lengths in most specimens less than 69 mm, but are greater than carapace lengths in animals larger than 70 mm). Few sperm were present in the epididymides of four T. coahuila with small testes in late July and August, but in the two males with greatly enlarged testes in late August, sperm were much more numerous. Sperm were most abundant in epididymal smears of four males in April. The epididymides of these turtles were slightly distended and contained a milky fluid, presumably semen, whereas the epididymides of turtles in July and August lacked any noticeable fluid.

Of the four males lacking sperm in the epididymides, two are clearly subadult (85.1 and 89.2 mm), whereas two appear to be adults on the basis of size (117.2 and 131.5 mm) and external appearance. Testes of the last two are very small, with combined testes weights of trace and 0.08 g, and volume displacements of 0.01 and 0.12 ml, respectively. The testes did not contain sperm. These two individuals were collected in the last week of July. Two other males that had testes of 0.07 and 0.15 g and 0.08 and 0.18 ml were caught at about the same time (26 July), but their epididymides contained sperm. It is possible that the two unusual males were actually immature or sterile. Mature sperm were found in the epididymides of *T. c. carolina* throughout the year (Altland, 1951), and in *T. o. ornata* throughout the activity season (Legler, 1960). However, Tinkle (1958b) discovered no sperm in the testes of 20 large male *Sternothaerus carinatus* and concluded that they were "out of season" when collected. Tinkle (1958b:44) further notes that, "The complete absence of spermatozoa was unusual, as a few generally may be found even in out of season males of other forms." An explanation of the apparent non-reproductive condition in the two unusual males is difficult because of limited data on the extent of the spermatogenic cycle in *T. coahuila*. The cycle may be in its early or middle stages in mid-summer, at a time when sperm have not yet matured (see below), so the last interpretation may be applied to the two males.

Seasonal change in testes size in turtles is generally coincident with the stage of spermatogenesis, the testes reaching maximum size at the height of the cycle before the spermatozoa enter the epididymides. In Michigan, the Stinkpot, Sternothaerus odoratus, had smallest testes in early May during the period of most active breeding (Risley, 1938). The spermatogenic cycle began in early to mid-June and the testes enlarged, reaching a maximum in July and August when spermatogenesis culminated. Ovulation in the female occurred in mid-May. Spermatozoa were most abundant in the testes in September. In October and November the testes underwent a gradual reduction as sperm were transferred to the epididymides for storage through hibernation. In Terrapene c. carolina from Pennsylvania and Maryland, Altland (1951) found that testes reached their greatest size in July and August. The cycle began in early June with increasing numbers of spermatogonia and reached its peak in July and early August. Spermatozoa were most prominent in August and early September and the cycle was largely completed by mid-September. In Kansas, spermatogenesis in T. o. ornata begain in early May with the presence of numerous spermatogonia in the seminiferous tubules (Legler, 1960). The cycle reached a peak in early September with the production of numerous spermatozoa, and was completed by the latter half of October. Testes were smallest in April immediately following hibernation, enlarged from April to early June, and then shrank in June following the period of most active mating. They enlarged again in July and August, reaching a maximum in early September, and became slightly smaller prior to hibernation in early October.

Seasonal fluctuation in testes size is evident in *T. coahuila* (Table 5). The testes were small in specimens from April and July, but had increased dramatically by late August in two of four specimens. The data on testes sizes and relative abundance of sperm indicate a spermatogenic cycle not greatly different from *T. c. carolina*, *T. o. ornata*, and *Sternothaerus odoratus*. However, on the basis of observed matings of *T. coahuila* in nature and under semi-natural conditions, and because of its unique habitat in a southern and thermal-spring environment which permits a more extended period of sexual activity than in more northern turtles, spermatogenesis may be extended for an unknown length of time into the winter. If this occurs, *T. coahuila* has a spermatogenic cycle different from the known cycle in the two species of *Terrapene* in the United States. Data are lacking for the more tropical *T. carolina mexicana* and *T. c. yucatana* of southeastern Mexico, and *T. n. nelsoni* and *T. n. klauberi* of western Mexico, as well as for other species of turtles from climates permitting more or less year-round activity.

Sexual Maturity and Seasonal Cycle - Females

Cagle (1944b) considered female *Pseudemys scripta*

Table 5. Mean sizes of testes of 10 mature male *Terrapene coahuila*. (Ranges in parentheses).

	Mean Testes diameter (mm)	Mean Weight of Both Testes (g)	Mean Volume of Both Testes (ml)
April (n = 4)	6.4 (5.0 - 9.0)	0.13 (0.05 - 0.31)	0.17 (0.09 - 0.30)
July (n = 2)	6.2 (6.0 - 6.3)	0.11 (0.07 - 0.15)	0.13 (0.08 - 0.18
August (n = 4)	10.4 (5.0 - 17.1)	1.13 (0.09 - 2.94	1.28 (0.10 - 3.40)

having follicles 15 mm in diameter as mature, and in *Chrysemys picta* used egg-laying as the criterion for maturity (Cagle, 1954). Tinkle (1961) determined sexual maturity in female *Sternothaerus odoratus* by the presence of enlarged ovarian follicles, ovulation scars in the ovary, or eggs in the oviduct. Legler (1960) noted that the uterine portion of the oviducts of *Terrapene o. ornata* became darkened in the breeding season, whereas oviducts of immature females were ordinarily pale. Female *T. coahuila* with one or more ovarian follicles larger than 5 mm in diameter were considered mature, but size and color of the oviducts was also used to indicate sexual maturity, especially in postreproductive females that lacked enlarged ovarian follicles. In 28 of 30 mature females, the uterine portion of each oviduct was black. All oviducts in mature females were noticeably thickened, and had larger, more expanded ostia than those of immature females. A female collected on 4 April 1966 may have been beginning its first reproductive season. The left oviduct was black while the right was light-colored, and there were two enlarged follicles in the left ovary. The female apparently would have ovulated two eggs, and presumably into the "mature" left oviduct.

Carapace lengths of 30 mature females ranged from 90.7 to 147.5 mm, mean 101.6 ± 2.1 mm. Based on this sample, carapace lengths of 95% of mature females in samples from the study area would be expected to fall between 97.3 and 105.9 mm.

The smallest mature female T. o. ornata found by Legler (1960) in Kansas had a plastron length of 107 mm, and only 47% of his sample were mature at a plastron length of 100 to 109 mm, most maturing when they had attained a plastron length between 120 and 129 mm. Male T. o. ornata become sexually mature at a smaller size than do females (Legler, 1960). This situation is reversed in T. coahuila, with females attaining sexual maturity at a significantly ($t = 2.03$, $P < 0.05$) smaller size than males.

Fifteen females of T. coahuila taken in the first week of April 1966, 10 in July 1965, and 9 in August 1965 are represented in the sample examined. Individuals in July and August did not differ in condition of their reproductive tracts and were combined. Seasonal comparisons were made between the April group and the July - August group. Two individuals from each group were considered subadult or immature, reducing the numbers to 13 mature females in April and 17 in July and August.

All 13 mature females in April were prereproductive and had not yet ovulated. These had heavier ovaries than females in July and August (Table 6), but the difference between them was not statistically significant ($t = 1.66$, $P > 0.10$). Weights of ovaries of T. coahuila were considerably less than those of T. c. carolina reported by Altland (1951) and of T. o. ornata (Legler, 1960). Ovarian weights of T. coahuila early in July tended to be greater than those

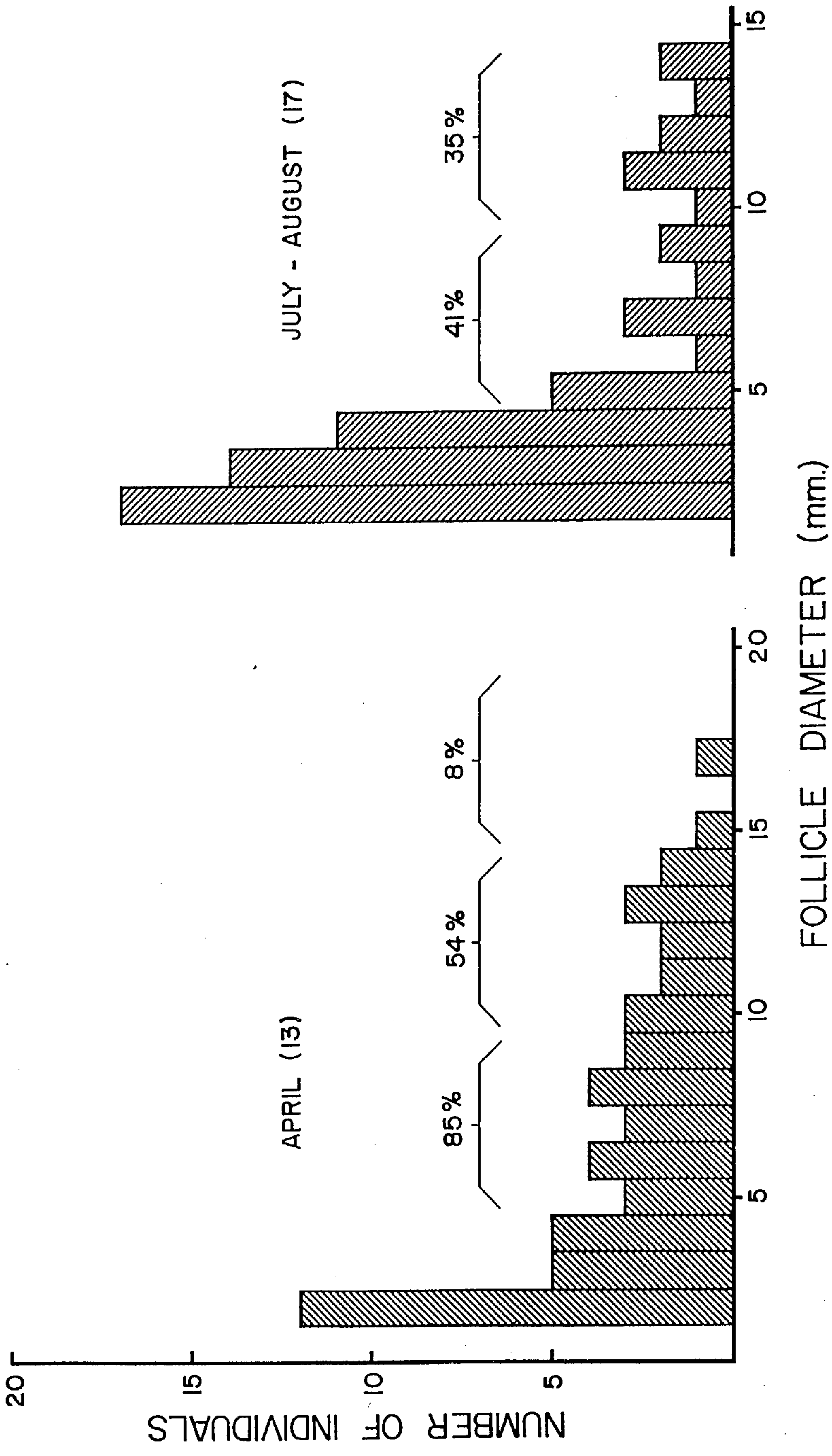
Table 6. Ovarian weight and number of follicles in ovaries of 30 mature female *Terrapene coahuila*.

	Mean Weight of Both Ovaries (g)	Mean Number of Ovarian Follicles > 1 mm
April (n = 13)	2.16 ± 0.57 (0.36 - 6.24)	8.1 ± 0.8 (3 - 14)
July - August (n = 17)	1.21 ± 0.27 (0.32 - 4.17)	11.8 ± 1.0 (5 - 21)

in late July and August. Many females in late July and August are probably postreproductive, having small ovaries in a period between a previous ovulation and the beginning of a new ovarian cycle. Although the carapace lengths of mature females in the July - August sample averaged slightly larger (103.4 mm) than those in the April sample (99.2 mm), there was no significant different in size between the two groups ($t = 0.98$, $P > 0.30$). For convenience, follicles were grouped into size classes as follows: 1 - 4 mm, 5 - 9 mm, 10 - 14 mm, and >15 mm. Follicles in the last three groups were considered enlarged. Figure 16 shows the distribution of follicle sizes in all mature females from both samples. Forty-four per cent more females in April than in July and August contained follicles in the 5 - 9 mm size range, and 19% more had follicles between 10 and 14 mm. Follicles in the latter size range were preovulatory. In addition, nearly twice as many females in April (69%) contained at least two follicles greater than 5 mm in diameter, compared to 35% of the females in July and August. In those females ($n = 15$) with two or more follicles 5 mm or greater in diameter, there was a significant correlation between the average diameter of the enlarged follicles and the weight of the ovaries ($F = 18.52$, $P < 0.01$).

No relationship appeared between the size of a turtle and the total number of follicles greater than 2 mm in the ovaries. This lack of correlation was found for both the

Figure 16. Follicle size distribution in ovaries of 30 mature female T. coahuila. Percentages of total number of individuals in each sample that contained follicles in arbitrary 5 mm size groups are shown.


APRIL (13)
85%
54%
8%
JULY - AUGUST (17)
41%
35%
NUMBER OF INDIVIDUALS
20
15
10
5
FOLLICLE DIAMETER (mm.)
5
10
15
20
5
10
15

April sample ($F = 0.53$, $P > 0.05$), and the July - August sample ($F = 1.15$, $P > 0.05$). However, females in July and August possessed a significantly greater ($t = 2.76$, $P = 0.01$) mean number of follicles per female than did the April females (Table 6). Most of these were small follicles, indicating that the majority of the turtles in the July - August sample were postreproductive, and suggesting that a new cycle may begin at that time. Legler (1960:550) reported that ". . . many minute follicles form on the germinal ridges of the ovaries" of female T. o. ornata in July or August. A further difference between the prereproductive April females and the largely postreproductive July - August females is obvious in the sizes of follicles present. Postreproductive July - August females possessed 26% more small follicles (1 - 4 mm) than did prereproductive April females. Conversely, females in April possessed 26% more enlarged follicles (>5 mm) than did the July - August females (Fig. 16) and 13% more follicles greater than 10 mm, which would probably have matured and been ovulated later in April or in early May. One female taken on 4 April 1966 had ovarian follicles 15 and 17 mm in diameter, and was believed to be on the verge of ovulation. These were the largest follicles found in any female in the total sample. Yolks of two oviducal eggs examined had average diameters of 16 and 17 mm, indicating the probable size attained by ova just prior to ovulation. Altland (1951) reported diameters of enlarged ovarian follicles during May in preovulatory T. c. carolina as large as 25 mm, and Legler (1960) considered that follicles of T. o. ornata mature between 16 and 20 mm in diameter.

An alternation of ovarian activity was noted in the 30 mature female T. coahuila. Fifteen females contained more follicles >2 mm in diameter in the left ovary as opposed to the right, 13 had more follicles in the right than the left, and two had the same number in each. While the total number of follicles in left vs right ovaries was nearly identical (151 left, 155 right), the 28 most-active ovaries contained a mean of 5.86 ± 0.43 follicles (range 2 - 12) and the 28 least-active ovaries had 3.86 ± 0.38 follicles (range 1 - 9). A highly significant difference ($X^2 = 10.96$, $P<0.005$) exists between the number of follicles in the 28 more-active vs. 28 less-active ovaries. This indicates that one ovary is usually more active than its partner in a given reproductive period. For example, a female on 9 July 1965 with three oviducal eggs had two corpora lutea in the right ovary and one in the left, while the left ovary contained 3 enlarged follicles representing the next set of eggs. This phenomenon was also noted in T. o. ornata from Kansas by Legler (1960).

Ovaries of T. c. carolina were heaviest in May when they contained 2 to 8 enlarged follicles (Altland, 1951). Ovulation normally occurred in June and July with a corresponding decrease in ovarian weight, but ovulation occurred as late as August 15. Follicles began to enlarge in July and August, following ovulation, with enlargment as late as September or October. Altland suggested that some of the enlarged follicles formed prior to hibernation were held over to the next reproductive season. The ovarian cycle of T. o. ornata in Kansas (Legler, 1960) is similar to that of T. c. carolina. Ovaries weighed most in March and April prior to ovulation, least in August and September, and increased again in October before hibernation. Ovulation occurred chiefly during May and June, but an estimated 33% of females appeared capable of a second ovulation in July. The cycle began in July or August with the formation of many small follicles. Ovarian follicles either grew nearly to maturity in the season preceding ovulation, or grew rapidly in the short period of approximately six weeks between spring emergence and ovulation (Legler, 1960).

Cagle (1944b:149) found ovaries of Pseudemys scripta elegans in Illinois containing enlarged follicles throughout the year, the only change in gross appearance of the ovary being a gradual increase in follicle size, which ". . . advances one set to the ovulatory stage each season." Weights of ovaries of Pseudemys scripta from Illinois, Tennessee, Kentucky, and Louisiana were greatest in May, and decreased greatly through June to July (Cagle, 1950). Some females in September and October contained enlarged follicles, suggesting follicular enlargment in autumn. Einem

(1956) reported enlarged follicles in female Kinosternon b. bauri from Florida in August and September, and Tinkle (1961) presented convincing evidence that female Sternothaerus odoratus form large follicles during summer which may be held over for ovulation the next year. Females collected in the winter had enlarged follicles which had formed during autumn and early winter.

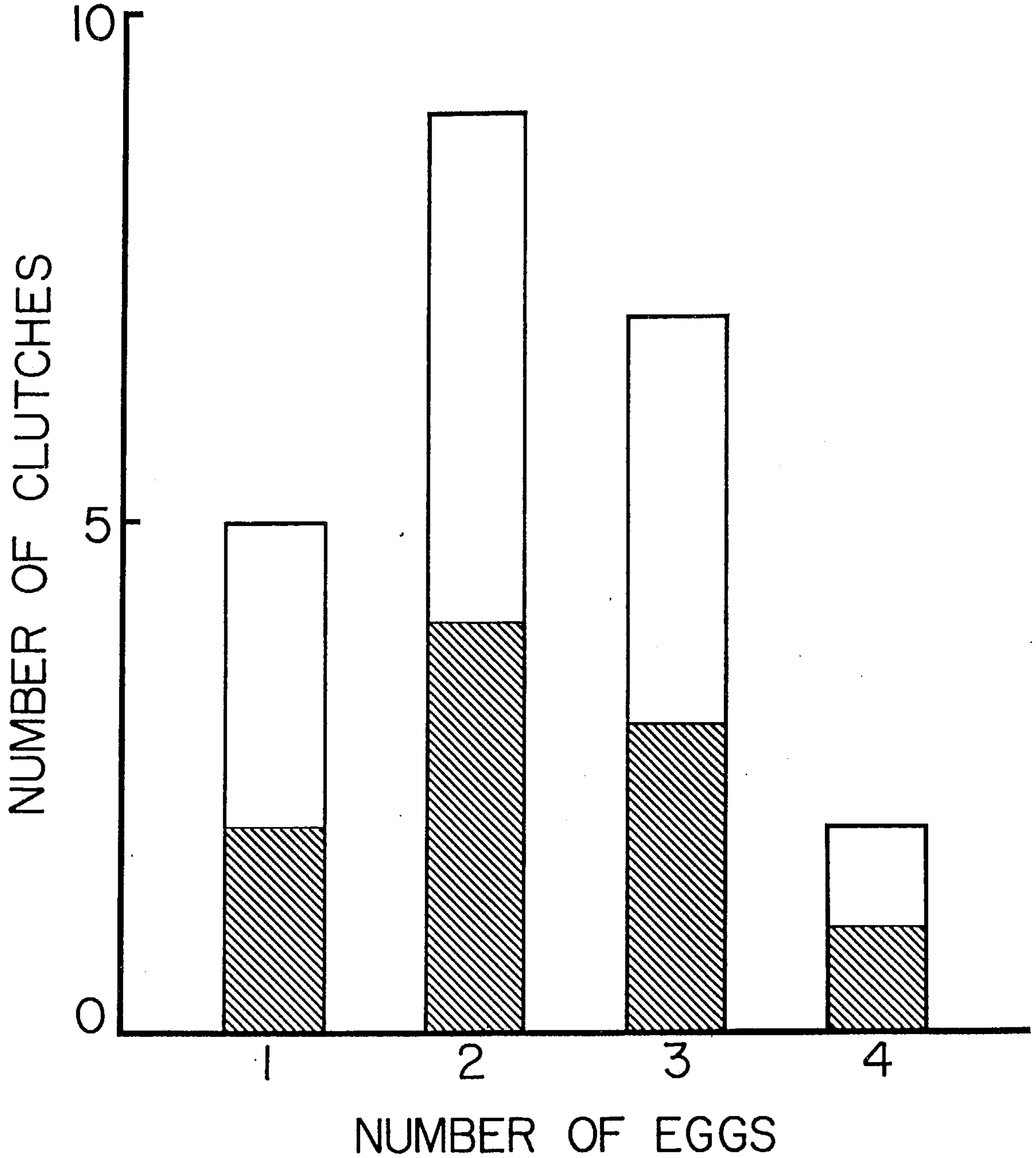
Several female T. coahuila with enlarged follicles were collected in late August. One, on 23 August 1965, had follicles 5 and 7 mm in diameter, and another on 30 August 1965 had three follicles measuring 5, 5, and 6 mm. On 24 August 1965 a female contained three enlarged follicles, two of which (11 and 12 mm) were approaching ovulatory size. It seems likely that in these females yolk deposition was occurring in late summer and early autumn. Ovulation of the two largest ova in the last female might have occurred in mid-September, but the smaller follicles in the first two females may have been held over until the following spring, as reported by Altland (1951) for T. c. carolina and Tinkle (1961) for Sternothaerus odoratus.

T. coahuila remains active throughout the year except for short periods of environmental extremes. Sexual activity occurs mainly from September to June. Follicular enlargement occurs between late August, when ovarian weights are low, and early April when ovaries are heavy and when nearly all mature females have one or more enlarged follicles (Table 6, Fig. 16). Follicles of females depositing clutches in autumn may undergo enlargement in late winter and in spring. Sperm from matings in autumn and winter probably are retained in the oviducts. Fertilization two and four years after insemination has been reported in _T_. _c_. _carolina_ by Finneran (1948) and Ewing (1943), respectively. Follicular atresia in _T_. _coahuila_ is not great. Tiny white follicles in the ovaries, which may have been atretic, were not counted. Only two slightly enlarged and discolored follicles were considered atretic. Both were in the same ovary of a female containing oviducal eggs on 9 July 1965. Altland (1951) observed follicular atresia most frequently in August in _T_. _c_. _carolina_, but he indicated that atresia did not account for a complete loss of enlarged follicles over the winter in that species. Legler (1960) observed brown, orange, or purplish atretic follicles in ovaries of many female _T_. _o_. _ornata_.

Clutch Size

Sixteen female _T_. _coahuila_ (six with large preovulatory follicles, seven with corpora lutea or enlarged follicles or both, and three with oviducal eggs or enlarged follicles or both) representing 23 actual or potential clutches indicate that, in the population studied, complements of 2 or 3 eggs are produced most frequently (Fig. 17) with an over-all mean clutch size of 2.3 (range 1 to 4).

Figure 17. Number of eggs in 23 actual or potential clutches of T. *coahuila*. Shaded portions represent actual clutches determined from counts of oviducal eggs and corpora lutea; unshaded portions represent potential clutches determined from counts of enlarged ovarian follicles.



10
5
0
NUMBER OF CLUTCHES
1
2
3
4
NUMBER OF EGGS

From 60 clutches of eggs laid by *T. c. carolina* near Washington, D.C., Allard (1935) reported clutch sizes of 2 to 7 eggs, and a mean of 4.2. Ewing (1933) counted 1 to 5 eggs (mean 3.0) in 14 clutches of *T. c. carolina* near Washington, D.C. in 1930 and 1931, and found a mean clutch size of 3.6, range 1 to 6, in 17 clutches in 1933 and 1934 (Ewing, 1935). Altland (1951) recorded 2 to 5 eggs in oviducts of *T. c. carolina* from Pennsylvania and Maryland. Legler (1960) found 2 to 8 eggs in 23 clutches of *T. o. ornata* in Kansas; mean clutch size was 4.7. These data indicate that *T. c. carolina* and *T. o. ornata*, living at more northern latitudes, have higher average clutch sizes than does the southern *T. coahuila*. Tinkle (1961) gives an average of 2.2 eggs in southern and 4.6 eggs in northern *Sternothaerus odoratus*. Clutch size decreases progressively as one moves south to lower latitudes. The small clutch (1 to 4, mean 2.7 eggs) of *T. n. nelsoni* from Nayarit, Mexico, recently reported by Milstead and Tinkle (1967), together with that reported here for *T. coahuila*, concur with Tinkle's data on *S. odoratus* and indicate that latitudinal variation in clutch size also occurs in *Terrapene*.

Seven of 10 female *T. coahuila* in July and August possessed corpora lutea in the ovaries, but had no oviducal eggs, indicating recent oviposition. In the three females with oviducal eggs (3, 4, and 2; mean 3.0 eggs per female), corpora lutea were cup-like structures, approximately 6 to

7 mm in diameter, and appeared similar to the corpus luteum of _T. c. carolina_ illustrated by Altland (1951). In each case, there was agreement between the number of corpora lutea in the ovary and the number of eggs in the oviduct on the corresponding side, so there was no indication of extra-uterine migration of ova to the contralateral oviduct as reported by Legler (1958) and Tinkle (1959a), and no indication that any eggs had been laid before the turtle was preserved. Altland (1951) noted degeneration of corpora lutea in some female _T. c. carolina_ while eggs were still in the oviducts, and atresia of corpora lutea was completed by August, shortly after the egg-laying period. Corpora lutea of _T. o. ornata_ undergo rapid involution and are barely discernible after two or three weeks following oviposition (Legler, 1960). The length of time that corpora lutea are maintained in reptiles is correlated with the egg-retaining habits of a species (Miller, 1959). In ovoviviparous and viviparous species the corpus luteum begins to regress before the end of the gestation period, and regression of the corpus luteum occurs shortly after egg-laying in oviparous forms. Miller (1948, 1959) drew no conclusion as to the possible function of the reptilian corpus luteum, and Tinkle (1958b), in using the term, neither assumed nor denied an endocrine function of the structure. I follow Tinkle (1958b) in the use of the term.

The large female containing four oviducal eggs had both oviducts, each containing two eggs, displaced to opposite sides of the body cavity, and the right ovary of this individual was also displaced and located in the left side of the body cavity near the left ovary. This individual was the largest turtle of either sex taken (147.5 mm carapace length), but it was not from the study area. Legler (1958) noted a similar phenomenon in T. o. ornata when oviducts contained large complements of eggs.

Six females in April, approaching their first ovulation of the season, had 2 to 4 preovulatory ($>$10 mm) follicles, mean 2.7. These follicles are thought to represent the first clutch. It could not be determined if slightly smaller follicles might have grown rapidly to be ovulated with the more enlarged follicles upon which the estimate is based, or if the large follicles thought to represent a clutch might have failed to ovulate. One female on 4 April 1966 contained follicles of two distinct size groups which possibly represented two future clutches. Ovulation seemed imminent for two follicles, with the other group of three representing a second clutch. Several other females in April also gave indications of capability for multiple clutches, containing five and six follicles greater than 5 mm in diameter that presumably represented two developing clutches.

Ovulation first occurs for most members of the population in April, oviposition in May (see "Egg-laying Season" below). Allowing sufficient time before June or early July for an additional set of ova to be ovulated and deposited, the 10 females taken between 3 July and 24 August 1965 provide evidence for second and third clutches in *T. coahuila*. Of the seven females with corpora lutea, four possessed 1 to 2 preovulatory follicles, and, of the three carrying oviducal eggs, two had 1 and 3 preovulatory follicles. Thus, six females were at a stage between a second ovulation, as indicated by corpora lutea, and a third ovulation, as indicated by preovulatory follicles. Three individuals had corpora lutea only. Based on these nine females (53% of July - August sample), plus the female in April with its second set of enlarged follicles, mean size of the second clutch is 2.4, range 1 to 4. Since it contained no enlarged follicles and therefore it could not be definitely determined whether a second clutch was represented, one female with two oviducal eggs on 26 August 1965 is not included. Probably not all females in the population would deposit second clutches, since some individuals in the July - August sample possessed neigher corpora lutea nor enlarged follicles. However, rapid disappearance of corpora lutea, and collection of females in an intermediate period as mentioned earlier, may influence this conclusion. The six females (35% of July - August sample) capable of depositing third clutches contained from 1 to 3 preovulatory follicles, mean 1.7.

Cagle (1944b) indicated that *Pseudemys scripta* may lay more than one clutch in a season, and estimated that the same species may deposit three clutches each season on the basis of the long laying season (April to July) and because females in spring usually had ovarian follicles in three or four distinct size groups (Cagle, 1950). *Chrysemys picta* females were thought by Cagle (1954) to produce 2 or 3 clutches in a single season. Some *Pseudemys scripta elegans* and *Graptemys pseudogeographica ouachitensis* females in Lake Texoma, Oklahoma, produce three clutches per season (Webb, 1961). Einem (1956) reported that *Kinosternon b. bauri* females in Florida produce two annual clutches, and Tinkle (1958b) presented evidence that *Sternothaerus carinatus* and *S. minor* in southeastern United States produce more than one clutch per season. Risley (1933) found that only one clutch per year is laid by *Sternothaerus odoratus* in Michigan, and Tinkle (1961) could find no direct evidence that this species produces more than a single clutch in any part of its range, although he noted that postreproductive females from southern populations had 66% more enlarged follicles than northern turtles, and this, coupled with a much longer breeding season at southern latitudes, indicated a potential for laying second clutches. Ewing (1935) reported a captive female *T. c. carolina* laying two clutches of eggs in the same season in two separate years. The time span between these layings was about three weeks in one instance, and six weeks in the other. The first may have been a case of extended egg retention since the intervening period was brief and the clutches were small (two eggs and one egg). Retention of eggs in oviducts has been reported by Risley (1933) for Sternothaerus odoratus, and by Cagle and Tihen (1948) for Deirochelys reticularia. Legler (1958) found evidence that T. carolina populations (subspecies not given) in southeastern United States produce more than one clutch of eggs per season. In Kansas, 11 female T. o. ornata (approximately 33%) in a sample of 34 during June and July had produced or would have produced two clutches of eggs in the same season (Legler, 1960).

Clutch sizes in T. coahuila decrease from a mean of 2.7 eggs in the first clutch to 2.4 in the second and 1.7 in the third. Smaller second clutches for box turtles have been reported by Legler (1960) who determined that second clutches of T. o. ornata averaged 3.5 eggs as compared to first clutches of 4.7.

Clutch sizes in turtles may vary with the size of the female. Although variable, in 12 T. coahuila with 13 potential clutches determined by counts of enlarged preovulatory follicles, 5 of 8 females between 90 and 100 mm in carapace length would have laid two eggs; 2 of 3 females 100 to 110 mm, three eggs; and 1 of 2 females over 110 mm, four eggs. There was also a direct correlation between body size and clutch size in the three females containing oviducal eggs (Table 7). Cagle (1944b, 1950) found a positive correlation between body size and clutch size in Pseudemys scripta, but in 1954 he reported no such correlation in Chrysemys picta. Smaller Kinosternon b. bauri contained fewer eggs than larger females (Einem, 1956). Tinkle (1961) grouped female Sternothaerus odoratus into large and small size groups, and a direct correlation existed between clutch size and body size. Legler (1960) compared plastron length with the number of eggs laid by 21 female T. o. ornata. A tendency for larger females to produce larger clutches was indicated, but extreme variability obscured the relationship.

Reproductive Potential

The estimate of the maximum reproductive potential used here refers to the maximum natality of Odum (1959:161): ". . . the theoretical maximum production of new individuals under ideal conditions." This potential can be estimated by counting the number of enlarged follicles that could be ovulated in one season and adding to this the number of oviducal eggs or corpora lutea, or both (Tinkle, 1961). Tinkle (1961) noted the difficulty in calculating the reproductive potential in turtles in which a new ovarian cycle may begin late in the season and result in enlarged follicles which may not be ovulated until the following season, and in which more than one clutch per year may be produced. Both of these phenomena are known to occur in T. c. carolina and T. o. ornata (Altland, 1951; Legler, 1960), and they occur also in

T. coahuila (see above). Tinkle (1961:72) further notes that ". . . counts of follicles, lutea, and eggs will give an estimate of the maximum [sic] egg production . . . but the actual production may be much lower." The maximum annual reproductive capacity of T. coahuila may amount to 11 eggs (maximum of four eggs in the first two clutches and three eggs in the third clutch).

Several difficulties in using this method for T. coahuila were apparent in addition to those mentioned by Tinkle: (i) it could not be determined accurately whether all the females collected in April had developed a full complement of potentially ovulatory follicles; (ii) because of the probable rapid disappearance of corpora lutea, it was impossible to determine if some postreproductive females had already ovulated, and, if so, how many eggs had been laid; and (iii) some postreproductive females lacked enlarged follicles, possibly because they were preserved before a new ovarian cycle had begun.

For females collected in April, the prereproductive potential, as estimated by counts of enlarged ovarian follicles in nine mature females having two or more follicles greater than 5 mm in diameter, was 3.9 eggs/female per season. However, T. coahuila produces more than one clutch of eggs per season, forming new follicles in each of three possible reproductive periods, so the above estimate seems low. The difference of 1.2 eggs between the prereproductive potential

(3.9) and the average first clutch size (2.7) further indicates early follicular enlargement for second ovulations. Fifty-three per cent of the July - August sample had produced or would have produced two clutches. In the estimated 35% of females producing three clutches of eggs per season, the mean reproductive potential, determined by adding the mean number of eggs in each clutch, is 6.8. Whether this estimated mean potential would be realized in any given season would depend on many environmental variables. In favorable years, more ova may mature and more clutches may therefore be produced.

As is true for clutch size, reproductive potential of Sternothaerus odoratus varies geographically (Tinkle, 1961). In comparing reproductive potential of T. n. nelsoni from western Mexico with T. o. ornata and T. c. carolina from middle and northern USA on the basis of average single (or first) clutch sizes produced in these populations, Milstead and Tinkle (1967) proposed that reproductive potentials may be lower in southern than in northern Terrapene. From the sample examined, they concluded that T. n. nelsoni produces one clutch annually, but state: ". . . it must be admitted that the southern turtles may produce more than one clutch per year, a possibility that can be determined only from seasonal sampling of the populations" (Milstead and Tinkle, 1967:183). In producing up to three clutches a year, the mean reproductive potential (6.8 eggs/female per season) realized by some T. *coahuila* females is below the potential of 8.2 (mean first and second clutch sizes added) realized by about one-third of the T. o. *ornata* population in Kansas (Legler, 1960), but is higher than the mean clutch size (reproductive potential) of 4.2 eggs/female per season in T. c. *carolina* at Washington, D.C. (Allard, 1935).

Egg-laying Season

The egg laying season may be determined from the dates when turtles are found with oviducal eggs or fresh corpora lutea (Tinkle, 1961). The earliest date of laying indicated by preserved specimens of T. *coahuila* was 3 July (corpora lutea), the latest date 26 August (oviducal eggs). One female in the series of turtles collected on 4 April 1966 had greatly enlarged follicles and most likely would have ovulated within a week of that date. Judging from this individual, and from the large follicles in the ovaries of the other prereproductive mature females in the April sample, ovulation occurs as early as the first week in April and may be concentrated in the last half of April. Legler (1960) noted that T. o. *ornata* normally retained eggs in the oviducts for two to three weeks before laying. If three weeks is added to the approximate earliest date of ovulation (early April), egg laying would begin in late April or the first week in May. The egg laying period continues to the first week in September, if one week is added to the latest date when a female was found with eggs (26 August). One female had two preovulatory follicles on 24 August, extending oviposition to the latter portion of September if ovulation occurred in early September. Allard (1935) reported 60 female *T. c. carolina* near Washington, D.C. deposited eggs between June 4 and July 13. At approximately the same latitude, 31 clutches of *T. c. carolina* were laid between May 28 and July 14 (Ewing, 1933, 1935). Altland (1951) noted that oviposition in this subspecies in Pennsylvania occurred primarily in June and July, but as late as August 15. *T. o. ornata* in Kansas nests chiefly in mid-June, but nesting may occur as early as the first week in May or as late as mid-July (Legler, 1960). Tinkle (1961) found that *Sternothaerus odoratus* in southeastern United States contained eggs from March through July, but that oviposition in northern Stinkpot populations is restricted to May and June.

Incubation periods of turtle eggs are subject to wide variation depending largely upon environmental temperatures. Allard (1948:319) found that eggs of *T. c. carolina* hatched in 52 days ". . . in the high summer temperatures of the laboratory", but incubation periods varied between 69 and 135 days in nests; 87 to 89 days was the average incubation period under natural conditions. Incubation periods varied from 69 to 103 days in *T. c. carolina* at Washington, D.C. (Ewing, 1933). Conant (1951) observed a female *T. c. carolina* in Ohio constructing a nest and laying eggs on 15 June 1934; hatching occurred on 29 September 1934, after 105 days. Ewing (1933) reported hatching of T. c. carolina in September and early October, and Allard (1948) found that hatching in this species did not occur before early September, with one clutch delayed to October.

Legler (1960) noted wide fluctuations in laboratory incubation periods of T. o. ornata eggs. At an average daily temperature of 32.8 C, the mean incubation period was 59 days (24 eggs). At 27.8 C the mean incubation period was lengthened to 70 days (21 eggs), and at 23.9 C to 125 days (4 eggs). Sixty-five days was thought to represent the typical incubation period for the Ornate Box Turtle in eastern Kansas under natural conditions. Eggs of the Ornate Box Turtle laid in mid-June would hatch in mid-August, but may be delayed until October in years when summer temperatures are cooler than normal (Legler, 1960).

Climatological data indicate that mean monthly temperatures in the seven month period May through November range from a low of 19.0 C in November to 29.4 C in August at Cuatro Ciénegas (Contreras, 1942). Mean temperatures during this period in 1965 ranged from 18.5 (November) to 29.5 (July) (Modesto de la Garza P., personal communication). Although nothing is known regarding nesting and incubation in T. coahuila, if the 65 day incubation period given by Legler (1960) can be assumed to approximate that of the Coahuilan Box Turtle in the period from May through November when environmental temperatures would generally correspond to temperatures given by Legler for an incubation period of that length, eggs laid in mid-May would be expected to hatch by mid-July. Assuming that laying had occurred on the dates when collected (9 July, 1 August, 26 August), and using this 65-day estimate, the projected dates of hatching of the eggs contained in the three gravid females in my sample would be September 12, October 4, and October 30. If the female with preovulatory follicles on 24 August had laid eggs in mid-September, hatching might have occurred between mid-November and early December. Actual lengths of incubation of T. coahuila eggs may be less than 65 days, especially in summer. In cooler months (October to December) the incubation period may be increased.

No nests of T. coahuila have been discovered. It seems likely that they are placed within the marshes, possibly in moist, soft soils of sedge tussocks, where micro-environmental conditions may differ widely from conditions indicated by air temperatures. Here, nest temperatures would be modified by the surrounding water and warmed by insolation. Hatchlings appearing from October to December from eggs laid in August or September, should not experience thermal difficulty in emergence. Average maximum air temperatures in November (26.3 C) and December (20.7 C) (Contreras, 1942) would provide suitable conditions for activity of hatchlings. Also, the relatively warm water of the marshes would mitigate environmental extremes even on the coldest days. A one to three-month old post-hatchling was discovered in the study area at mid-day on 15 October 1966. The juvenile was sunning on a Chara mat in a marsh; nearby water temperature was 23.8 C, air 20.0 C. Sexton (1957:230) found two hatchling common snapping turtles, Chelydra s. serpentina, active in October in Michigan when the air was 11.7 C, and he states: "Evidently cool temperatures do not inhibit emergence from the nest." Extended periods of incubation (230 days) as reported by Driver (1946) for T. c. carolina, or over-wintering in the egg by hatchling turtles (Myers, 1952; Sexton, 1957) would not be expected to occur in T. coahuila living in a relatively warm climate.

Eggs

Nine oviducal eggs from oviducts of three preserved female T. coahuila are ellipsoidal and white. The shell is smooth to the touch, but finely granulated when viewed under a dissecting microscope. Dimensions and weights of the eggs are presented in Table 7. Many reptile eggs, including those of Terrapene, expand during the course of incubation by absorbing water (Cunningham and Hurwitz, 1936). Cunningham and Huene (1938) found that T. c. carolina eggs gained an average of 28% in weight, and Legler (1960) showed that T. o. ornata eggs increased by an average of 3 g in weight and 3 mm in width during incubation. Thus, data on reptile eggs are not strictly comparable unless their age and state of incubation are known (Cagle, 1953). This should be kept in

Table 7. Size of eggs in three clutches obtained from oviducts of female *Terrapene coahuila*. (Mean ± 1 SE).

Date Preserved	Carapace Length of Female	Length (mm)	Width (mm)	Weight (g)
9 July	116.0	31.2	15.8	4.44
		30.9	16.6	4.71
		30.5	16.8	4.87
1 August	147.5	34.5	17.6	6.21
		34.6	18.2	6.76
		36.3	17.9	6.81
		34.8	17.2	6.28
26 August	93.4	33.5	16.1	5.51
		32.8	16.2	5.35
		33.2 ± 0.67	16.9 ± 0.28	5.66 ± 0.30

mind in considering the following comparisons of egg sizes.

The following sizes of eggs of *T. c. carolina* have been reported: length, 28 - 40 mm; width, 19 - 21.5 mm (21 eggs, Allard, 1948); length, 30.5 - 35.0 mm; width, 18.5 - 19.0 mm (54 eggs, Cahn, 1937). Egg sizes of *T. c. bauri* (length 35 - 38.5, width 19.8 - 21.0 mm) and *T. c. major* (length 37 - 38.4, width 21.5 - 22.4 mm) are given by Carr (1952), and Crooks and Smith (1958) gave dimensions for several eggs of *T. c. triunguis* (length 32 - 34, width 23 - 25 mm). The last three fall within the ranges given above for *T. c. carolina*. Legler (1960) gave the mean sizes of 42 eggs of *T. o. ornata* within 24 hours after laying or removed from oviducts as follows: length, 31.3 - 40.9 mm; width, 20.0 - 26.3 mm. Mean size of 17 eggs of *T. n. nelsoni* was 47 x 27 mm (Milstead and Tinkle, 1967).

Lengths of *T. coahuila* eggs (Table 7) approximate the lengths reported by Allard (1948) for *T. c. carolina*, but are slightly less in width. From accounts in the literature, eggs of *T. c. bauri*, *T. c. major*, *T. o. ornata*, and *T. n. nelsoni* are all larger than the eggs of *T. coahuila*, while those of *T. c. triunguis* seem to be of approximately equal length. The mean weight of the nine preserved eggs of *T. coahuila* (5.66 g) is less than weights of *T. c. carolina* eggs (8.4 g, Allard, 1948; 9.24 g, Cunningham and Huene, 1938) and *T. o. ornata* eggs (10.09 g, Legler, 1960).

FOOD HABITS

References in the literature to the food of *Terrapene coahuila* are those of Williams (1960) and Webb et al. (1963). Williams (1960) noted that captive Coahuilan box turtles ate dead or live sunfish and roaches. One turtle succeeded in capturing a live fish in shallow water. Webb et al. (1963) stated that *T. coahuila* is omnivorous and a scavenger on the basis of a wide variety of foods consumed by captives. The observation that wild-caught Coahuilan box turtles defecated ". . . large amounts of rhomboidal seeds " (Webb et al., 1963:96) provides the only clue to the diet of the species in nature.

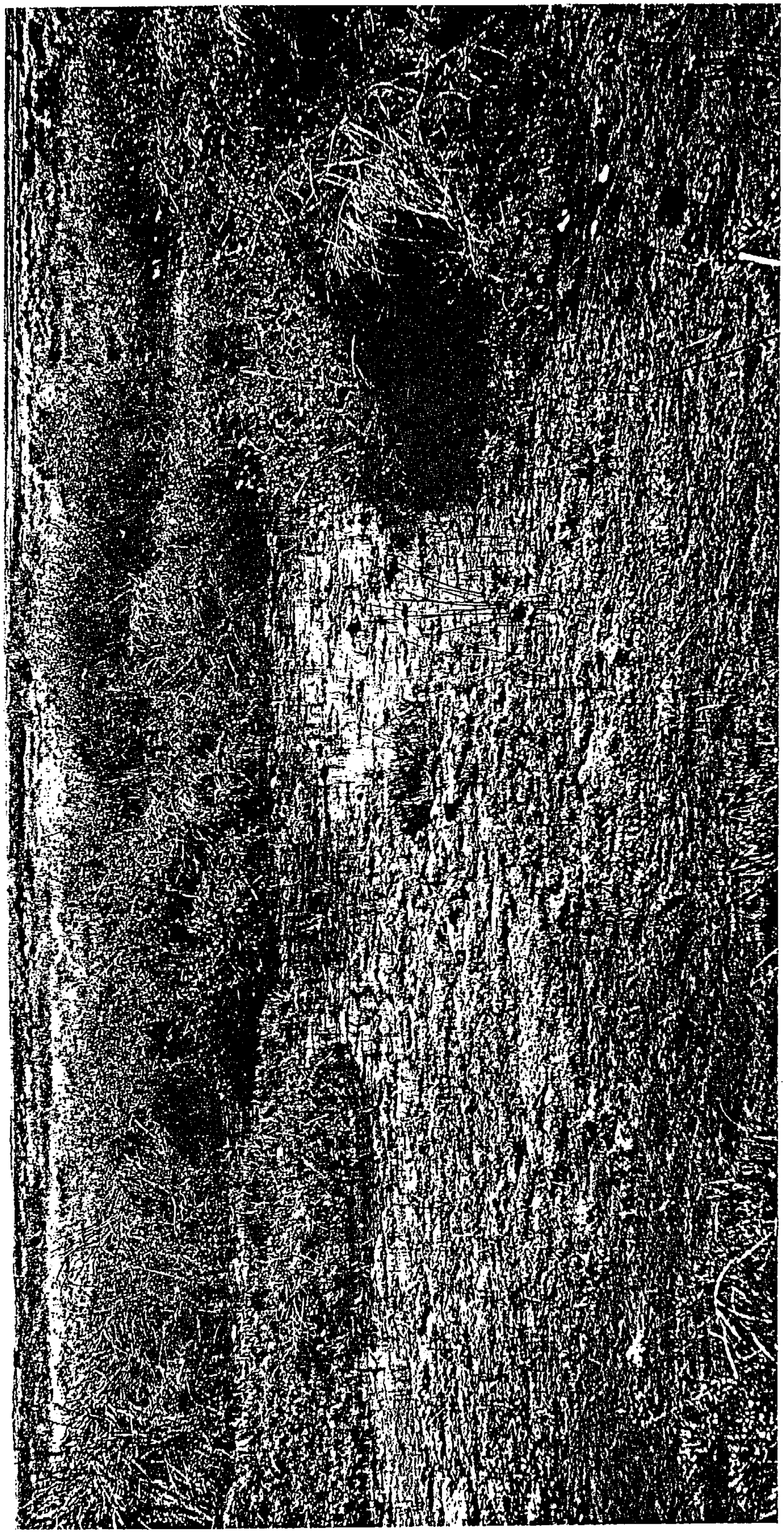
Foraging Behavior

Several Coahuilan box turtles were observed foraging for varying periods in nature. Although the vast majority of turtles captured were in shallow water within the marshes, only a few of these were observed long enough to gain some idea of the normal pattern of feeding. Visibility in a marsh was limited because of the thick growth of *Eleocharis* and *Scirpus*, the principal plants. By walking around and through a marsh, turtles were discovered largely by chance. Coahuilan box turtles are wary and have acute eyesight for large moving objects at distances of 30 meters or more. Thus, unless a marsh was approached carefully, an intruder might be seen while still too far away to observe the turtle closely, and it would disappear. Probably the keen eyesight of box turtles prevented many of them from being seen and captured.

When a turtle saw me, it would either stop foraging and remain motionless, or would immediately begin to burrow into the substrate. Infrequently, individuals would run for a distance of up to a meter toward dense vegetation, usually toward the center of the marsh, before digging into the mud bottom. Many turtles thrust themselves into the mud so rapidly that the rear of the shell and hind legs tilted upward at an angle of 45 degrees or more, and the animal literally appeared to dive into the mud. Such escape reactions occur rapidly, in a few seconds, and unless the turtle is retrieved immediately, the spot of disappearance may be lost and the escape completed.

Two marshes provided areas suitable for observation. The south and west edges of marsh 11 were relatively open, with areas of shallow water and scattered Eleocharis that was closely cropped by horses. A second marsh, N-3, was essentially open with an expanse of shallow water and beds of Chara and grazed Eleocharis around the perimeter, providing an unusually good situation where turtles were easily seen (Fig. 18). A crude blind, consisting of green canvas, was constructed on the south edge of this

Figure 18. East view of marsh N-3, 27 January 1966 at 11:10 AM. Mats of *Chara* are in foregound; a foraging male *T. coahuila* is at upper right of center. Air temperature was 10.2 C, water 26.9 C. Body temperature of the turtle was 26.7 C. A horse is visible in left background.



marsh, but appeared unsatisfactory, possibly because box turtles were aware of it. Careful approaches were made to the edges of these two marshes and foraging turtles were observed with binoculars. Rarely, busily feeding turtles could be approached to within one meter.

Foraging turtles moved quickly but deliberately through shallow water (Fig. 18). Water depth generally varied between 2 and 6 cm so that nearly the entire body of the turtle, or at least the top of the carapace, remained above the water level. The back of a foraging turtle was usually dry. The head was nearly always held below the water surface and the turtle moved forward, scanning underwater. Forelimbs were frequently employed to dig and pull at vegetation, moving plant material to the sides with forward, then with backward lateral thrusts of the front feet. Chara and basal portions of Eleocharis were moved in this manner while the head investigated the cleared area and the turtle nipped at portions of uprooted plant material or at exposed aquatic animals. It was estimated that once every two minutes, the turtle would pause to raise its head out of the water, extending the neck cautiously to survey the surroundings in several directions. These pauses usually lasted only several seconds, but their length would be increased if an intruder was suspected. Thus, on several occasions I was able to approach a feeding turtle to within one meter and observe it until it raised its head. It would survey me attentively for a long period, usually several minutes, remaining motionless. If I moved, it would either withdraw its head and limbs into the shell and remain motionless, or would attempt to escape by running or by burrowing into the mud bottom.

Between 21 July and 29 July 1965, ten observations of foraging turtles were made at the edge areas of marsh 11. Four were between 6:30 and 7:30 AM and six between 4:45 and 7:25 PM on different days. Morning patterns of foraging did not seem to differ from those in the evening. Cloacal temperatures varied between 26.3 and 32.3 C with broad overlap between morning and evening, and differences in rates of movement were not apparent. Once, a male climbed partially out of water onto a raised patch of Eleocharis and stalked and suddenly lunged at an unseen object in the vegetation. This individual foraged with its head extended underwater, intently looking for periods up to a minute, largely motionless. Another male climbed out of water onto a clump of sedge and investigated several Eleocharis stems about 6 cm above the water, but it did not eat them. An individual moved into channels between clumps of sedge, forceably snapping at and tugging on plant material with such force that the body jerked with each effort to pull the material free. A garter snake (Thamnophis sp.), apparently disturbed by the turtle, climbed up onto sedges above the turtle and disappeared.

On 21 July 1965, from 6:25 to 7:15 PM, a female in marsh 11 was observed from a distance of approximately one meter. The turtle moved in shallow water, pushing with its forefeet at the edges of clumps of vegetation and biting at the base of Eleocharis and mats of Chara. Several times it climbed partially out of water, pulling apart plant material and muddy debris with its forefeet, biting at stalks of sedge exposed in this manner. For approximately 20 minutes this individual utilized an area of only 25 or 30 cm^2. It was intent on foraging, pausing briefly with head raised every 2 to 3 minutes. It did not seem alarmed by my presence.

On 22 July 1965, from 7:00 to 7:45 AM, another female was observed from a distance of about six meters in a nearby area of marsh 11. This individual moved approximately three meters while foraging among clumps of Eleocharis, turning frequently and following narrow channels through the vegetation. Use of the forelegs in exposing places for feeding, and frequent pauses to survey its surroundings, were typical.

On 11 December 1965 at 2:35 PM in marsh 2-A, a female T. coahuila was feeding at the basal portion of an Eleocharis clump that was raised above a small pool of shallow water. This turtle pawed and bit at the roots and mud of the clump, apparently eating plant material. Cloacal temperature of the individual was 23.1 C; water was 22.7, and air 21.4 C.

In four observations, two or more box turtles were foraging in the same vicinity. Usually only one turtle was initially seen and watched, but when observations ceased and I moved forward to secure the individual, a second turtle was nearby. Twice, a male and a female were involved, while in another instance, a male was observed but the second individual escaped. On one occasion, three turtles, all females, were within three meters of each other.

Composition of the Diet

The food of _T. coahuila_ was determined by analysis of the contents of digestive tracts of 48 individuals, 14 males and 34 females. Twenty-nine were collected in July and August 1965, and 19 in April 1966. Individuals represented in the sample were collected from marshes (37), roads (5), marsh pools of the Río Mesquites (5), and posas (1). All turtles were of subadult or adult size.

Turtles were preserved initially in 10% formalin and later washed and transferred to a 50% isopropyl alcohol solution. Upon dissection the entire digestive tract was removed, a longitudinal cut was made through the length of the stomach wall, and the digestive tract was stored for one to two weeks prior to examination. Determinations of food items were made to order and family, and in some cases to genus and species. Methods were similar to those described by Berry and Bullock (1962). Individual items were sorted and counted with the aid of a dissecting microscope and volumes of major food items were determined by placing specimens in a 12 ml graduated cylinder, after removing excess isopropyl alcohol with an absorbent paper towel, and adding a known volume of 50% isopropyl alcohol from a pipette. The difference between the cylinder reading and the volume added gave the volume of the item. Plant material was lumped into a single category for volume determination. Intestinal contents were removed and placed in shallow plastic petri dishes after washing out dirt and other debris through cheesecloth strainers. Because items were often partially digested and fragmentary, no attempt was made to count individuals or measure volumes of organisms from the intestines.

Methods of presentation of data follow Larimore (1957): (i) percentage of stomachs in which each kind of food occurred (frequency of occurrence); (ii) mean number of items of each kind of food in stomachs containing the food; (iii) mean of the percentages of volume comprised by each of the kinds of food in stomachs containing the food; and (iv) percentage of the total volume represented by each kind of food.

Three of the 48 stomachs were empty and calculations presented in Table 8 and shown graphically in

Table 8. Organisms found in stomachs of 45 Terrapene coahuila containing food. Stages abbreviated: N., nymph; L., larva; P., pupa; A., adult. Ranges in parentheses.

	Frequency of Occurrence	Average Number of Organisms in Stomachs Containing Them	Average Percentage Volume of Organisms in Stomachs Containing Them	Percentage of Total Volume
Plant material (unspecified)	84.4			45.61
Ephemeroptera				
Baetidae (n.)	20.0	18.8 (1 - 76)	9.0 (1.2 - 24.1)	2.31
Unidentified (n. & a.)	4.4	2.0 (1 - 3)	2.2 (1.6 - 2.7)	0.04
Odonata				
Aeshnidae (n.)	2.2	3	13.1	0.27
Agrionidae (n.)	24.4	2.0 (1 - 6)	8.1 (1.9 - 23.3)	1.84
Gomphidae (n.)	4.4	2.0 (1 - 7)	27.3 (19.6 - 35.0)	1.09
Libellulidae (n.)	26.7	2.2 (1 - 7)	30.1 (tr. - 95.5)	7.14
Unidentified (n.)	2.2	1	24.5	0.94
Orthoptera				
Acrididae (n. & a.)	4.4	1.0	13.3 (12.3 - 14.2)	1.07
Hemiptera				
Belostomatidae (a.)	2.2	1.0	23.9	0.56
Nabidae (a.)	2.2	1.0	4.5	0.05
Naucoridae (n. & a.)	24.4	2.4 (1 - 13)	10.5 (0.6 - 41.2)	2.03
Pentatomidae (a.)	2.2	2.0	31.7	0.48
Veliidae (a.)	4.4	2.0	0.9 (0.8 - 1.1)	0.05
Unidentified (n. & a.)	8.9	1.0	0.7 (0.5 - 1.0)	0.04
Coleoptera				
Curculionidae (a.)	24.4	4.6 (1 - 21)	25.2 (tr. - 98.4)	8.98
Dytiscidae (l.)	4.4	1.5 (1 - 2)	23.9 (4.2 - 43.5)	0.44

Table 8. continued

	Frequency of Occurrence	Average Number of Organisms in Stomachs Containing Them	Average Percentage Volume of Organisms in Stomachs Containing Them	Percentage of Total Volume
Dytiscidae (a.)	6.7	1.7 (1 - 3)	1.9 (tr. - 5.4)	0.04
Hydrophilidae (a.)	11.1	1.8 (1 - 4)	6.9 (1.2 - 25.1)	1.57
Limnebiidae (a.)	4.4	10.0 (1 - 19)	2.9 (2.7 - 3.1)	0.06
Oedemeridae (a.)	4.4	1.0	6.5 (3.8 - 9.1)	0.17
Staphylinidae (a.)	2.2	1.0	0.5	0.02
Tenebrionidae (a.)	2.2	1.0	3.3	0.12
Unidentified	2.2	1.0	9.1	0.27
Trichoptera				
Hydroptilidae (l.)	4.4	1.0	0.9 (0.9 - 1.0)	0.07
Lepidoptera				
Microlepidoptera (a.)	2.2	1.0	0.9	
Unidentified (l.)	2.2	1.0	14.3	
Diptera				
Chironomidae (l.)	6.6	1.7 (1 - 3)	0.7 (0.2 - 1.1)	0.04
Culicidae				
Chaoborinae (l.)	15.6	1.9 (1 - 4)	0.9 (0.3 - 2.4)	0.14
Culicinae (l.)	2.2	1.0	0.3	tr.
Culicidae (p.)	6.7	2.0 (1 - 3)	0.9 (0.7 - 1.2)	0.06
Stratiomyidae (l.)	64.4	5.4 (1 - 26)	29.9 (3.1 - 98.8)	18.59
Stratiomyidae (p.)	2.2	1.0	6.3	0.24
Tipulidae (l.)	6.7	1.0	8.8 (1.6 - 18.0)	0.46
Unidentified (all stages)	6.7	1.0	0.4 (0.3 - 0.4)	0.04

Table 8. continued.

	Frequency of Occurrence	Average Number of Organisms in Stomachs Containing Them	Average Percentage Volume of Organisms in Stomachs Containing Them	Percentage of Total Volume
Hymenoptera				
Apoidea (a.)	2.2	2.0	1.2	0.07
Formicidae (a.)	8.9	12.0	7.6 (0.5 - 27.7)	0.53
Insecta				
Unidentified (all stages)	11.1		3.6 (tr. - 11.2)	0.50
Arachnida				
Araneae - Argiopoidea	8.9	1.0	14.9 (0.6 - 43.5)	1.21
Crustacea				
Amphipoda - Talitridae	17.8	20.9 (1 - 141)	5.5 (0.3 - 35.7)	0.45
Isopoda - Armadillidiidae	4.4	1.0	16.9 (13.8 - 20.0)	0.46
Isopoda - Sphaeromidae	2.2	1.0	35.7	0.24
Ostracoda - Cypridae	22.2	1.3 (1 - 4)	0.9 (tr. - 2.3)	0.14
Mollusca				
Gastropoda - Hydrobiidae	15.6	1.3 (1 - 2)	0.4 (tr. 1.6)	0.04
Cyprinodontiformes				
Cyprinodontidae	2.2	1.0	47.4	0.22
Poeciliidae	2.2	1.0	5.5	0.31

Figure 19 are based on 45 stomachs actually containing food. The total volume of all food items in the stomachs ranged from 0.19 to 2.54 ml, mean 0.92 ± 0.09 ml. Volumes of intestinal contents were not measured, but averaged considerably more than stomachs; estimates ranged from 2 to 50 ml.

Ranking of food items for the combined sample of 45 stomachs containing food was done on the basis of percentage of the total volume. This method of presentation was thought to represent most accurately the major components of the diet. Frequency of occurrence, combined with the mean of the volume percentages for the July - August sample vs. the April sample, show the relative importance of the various foods in the diet (Table 9). Ostracods, amphipods, and chaoborin midge larvae, although they occurred with a frequency comparable with the other groups listed, were not considered to be important items on a volume basis and are not included in Table 9.

While the percentage of total volume and frequency of occurrence are valid methods for interpopulation or interspecific comparisons in food habits, the mean number of items and the mean of the percentages of volume are instructive in estimating the value of a food item to those individuals that utilized the item. For example, a total of 167 amphipods were found in eight turtles, giving a mean of 20.9 amphipods for those stomachs in which they

Figure 19. Composition of diet by percentage of total volume of food in stomachs of 45 _T_. _coahuila_.

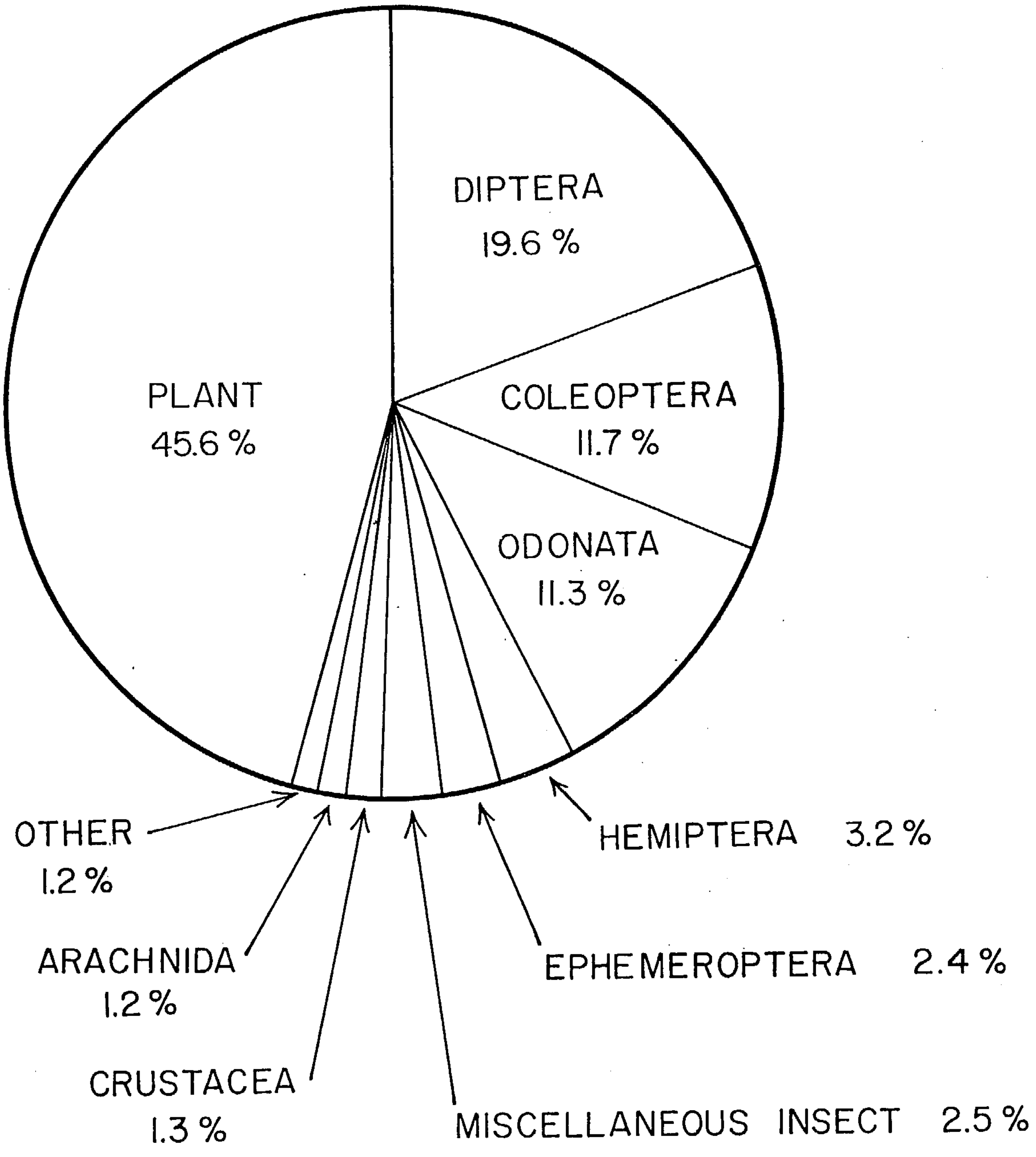

DIPTERA
19.6 %
PLANT
45.6 %
COLEOPTERA
11.7 %
ODONATA
11.3 %
HEMIPTERA 3.2 %
EPHEMEROPTERA 2.4 %
MISCELLANEOUS INSECT 2.5 %
CRUSTACEA
1.3 %
ARACHNIDA
1.2 %
OTHER
1.2 %

Table 9. Most important food items found in stomachs of 45 *Terrapene coahuila*. See text for methods of presentation. Stages abbreviated: N., nymph; L., larva; P., pupa; A., adult.

Food Item	Frequency of Occurrence	Average Percentage Volume
April Sample (n = 19)		
Plant Material	84.2	56.8
Stratiomyidae (l.)	79.0	29.7
Agrionidae (n.)	36.8	9.2
Libellulidae (n.)	36.8	26.0
Baetidae (n.)	31.6	7.0
Naucoridae (n. & a.)	26.3	6.5
July and August Sample (n = 26)		
Plant Material	84.6	45.5
Stratiomyidae (l.)	53.9	36.6
Curculionidae (a.)	26.9	38.6
Naucoridae (n. & a.)	23.1	13.9
Libellulidae (n.)	19.2	35.7
Agrionidae (n.)	15.4	6.0
Formicidae (a.)	15.4	7.6
Baetidae (n.)	11.5	13.2
Hydrophilidae (a.)	11.5	9.7

Table 9. continued.

Combined Sample (n - 45)		
Foot Item	Percentage of Total Volume	Total Number of Items
Plant Material	45.61	
Stratiomyidae (l.)	18.59	158
Curculionidae (a.)	8.98	51
Libellulidae (l.)	7.14	26
Ephemeroptera (n. & a.)	2.35	173
Naucoridae (n. & a.)	2.03	26
Agrionidae (n.)	1.84	22
Hydrophilidae (a.)	1.57	9
Crustacea	1.29	183
Araneae	1.21	4
Other Coleoptera (l. & a.)	1.12	33

occurred. The mean is strikingly high because of one individual containing 141 amphipods (see below). Amphipods, however, made up less than one-half of one per cent of the total volume for all food items. Average numbers of baetid mayfly nymphs, ants, and limnebiid beetles indicate that they were important to certain individuals, but these items assume a greater importance in the over-all diet than is actually the case when compared by this method. Cyprinodontid fishes, sphaeromid isopods, pentatomid bugs, gomphid dragonfly nymphs, belostomatid bugs, dytiscid beetle larvae, and grasshoppers were each found in only two stomachs at most. These food groups were importnat to some individuals in which a single item frequently comprised a large percentage of the volume in stomachs otherwise nearly lacking any other food.

Based on percentage of total volume, insects (50.7%), and plant material (45.6%) are by far the most important components of the diet (Fig. 19). Crustaceans (1.3%), spiders (1.2%), and fishes (0.5%) are relatively much less important. Plant material was in 84.4% of the stomachs and consisted of the following kinds with the frequency of occurrence of each: _Eleocharis_ _rostellata_, 64.4%; _Juncus_ spp., 17.8%; mushroom, 15.6%; _Chara_ spp., 11.1%; and large, unidentified seeds, 6.7%.

Several groups of insects are prominent in the over-all diet. Twenty-nine families representing nine orders were identified (Table 10). Nineteen of these families have one or more aquatic stages in their life cycles. Stratiomyid fly larvae occurred in nearly two-thirds (64.4%) of all stomachs containing food, and were the most important animal food in the diet (18.6% of total volume). Stratiomyid larvae are relatively large (1 - 2 cm long), many species living in shallow, stagnant pools or in mud. Adult curculionid beetles were in almost one-fourth (24.4%) of stomachs and were an important component by volume (almost 9.0%). Although the adults are not truly aquatic, the larvae of some species of these beetles live in the stems or roots of aquatic plants. Libellulid dragonfly nymphs were present in more than one-fourth of the stomachs (26.7%) and comprised over 7% of the total volume. Nymphs of dragonflies and damselflies are aquatic, and might be most subject to predation by T. coahuila when crawling out of the water onto a plant stem to undergo the final molt. Odonata adults are frequently observed in and around marshes in the study area. Naucorid nymphs and adults made up the bulk of the hemipterans recorded. These bugs may be eaiser for box turtles to catch, as they move more slowly through submerged vegetation, than other groups of aquatic hemipterans occasionally eaten (notonectids, belostomatids, and veliids). Baetid mayfly nymphs occurred in one-fifth (20.0%) of the stomachs, making up almost all of the 2.35% of total volume of mayflies. Most

Table 10. Taxonomic distribution and number of organisms found in digestive tracts of 48 *Terrapene coahuila*. Stages abbreviated: N., nymph; L., larva; P., pupa; A., adult.

	Stomach (n = 45)		Intestine and Rectum (n=48)
	Number in which found	Total Number of Items	Number in which found
Plant Material	38		48
Ephemeroptera			
Baetidae (n.)	9	169	0
Unidentified (n.&a.)	2	4	2
Odonata			
Aeshnidae (n.)	1	3	0
Agrionidae (n.)	11	22	14
Gomphidae (n.)	2	8	4
Libellulidae (n.)	12	26	10
Unidentified (n.)	1	1	2
Orthoptera			
Acrididae (n.&a.)	2	2	1
Hemiptera			
Belostomatidae (a.)	1	1	3
Nabidae (a.)	1	1	0
Naucoridae (n.&a.)	11	26	30
Nepidae (a.)	0	0	2
Notonectidae (a.)	0	0	1
Pentatomidae (a.)	1	2	1
Podopidae (a.)	0	0	2
Veliidae (a.)	2	4	2
Unidentified (n.&a.)	4	4	5
Coleoptera			
Curculionidae (a.)	11	51	22
Chrysomelidae (l.)	0	0	1
Dytiscidae (l.)	2	3	5
Dytiscidae (a.)	3	5	1
Hydrophilidae (a.)	5	9	8
Limnebiidae (a.)	2	20	0
Oedemeridae (a.)	2	2	0
Staphylinidae (a.)	1	1	0
Tenebrionidae (a.)	1	1	0
Unidentified (a.)	1	1	8

Table 10. continued.

	Stomach (n = 45)		Intestine and Rectum (n=48)
	Number in which found	Total Number of Items	Number in which found
Trichoptera			
Hydroptilidae (l.)	2	2	0
Lepidoptera			
Microlepidoptera (a.)	1	1	0
Unidentified (l.)	1	1	1
Diptera			
Chironomidae (l.)	3	5	0
Culicidae			
Chaoborinae (l.)	7	13	0
Culicinae (l.)	1	1	0
Culicidae (p.)	3	6	0
Stratiomyidae			
Potamidinae (l.)	3	42	0
Stratiomyinae (l.)	29	116	39
Stratiomyidae (p.)	1	1	0
Tipulidae (l.)	3	3	0
Ephydridae (p.)	0	0	1
Unidentified (all stages)	3	3	2
Hymenoptera			
Apoidea (a.)	1	2	1
Formicidae (a.)	4	48	13
Insecta			
Unidentified (all stages)	5		9
Arachnida			
Araneae - Argiopoidea	4	4	0
Crustacea			
Amphipoda			
Talitridae			
Hyalella azteca	8	167	3
Isopoda			
Armadillidiidae			
Armadillidium vulgare	2	2	4

Table 10. continued.

	Stomach (n = 45)		Intestine and Rectum (n=48)
	Number in which found	Total Number of Items	Number in which found
Sphaeromidae	1	1	1
Ostracoda			
Cypridae	10	13	13
Mollusca			
Gastropoda			
Hydrobiidae			
Durangonella sp. and *Paludiscala* sp.	7	9	9
Cyprinodontiformes			
Cyprinodontidae			
Cyprinodon sp.	1	1	1
Poeciliidae			
Gambusia marshi	1	1	0
Serpentes			
Colubridae			
Natrix erythrogaster	0	0	1

of the insects eaten by _T. coahuila_ were presumably obtained directly from the water of marshes, with the exception of curculionid beetles and other terrestrial forms encountered rarely during overland movements or possibly after having fallen into the water from nearby vegetation.

Remains of a juvenile Blotched Water Snake, _Natrix erythrogaster transversa_, were in the intestine of a female _T. coahuila_ collected in a marsh on 23 August 1965. Aside from fishes, this was the only record of predation on a vertebrate. Except for partial digestion, the snake appeared fresh and was probably eaten alive or after being recently killed. Other reptiles and amphibians observed within marshes were the Ground Skink, _Lygosoma laterale_, Ribbon Snake, _Thamnophis sauritus_, and Leopard Frog, _Rana pipiens_. None of these was present in any specimen of _T. coahuila_ examined. Several authors have reported _T. ornata_ and _T. carolina_ feeding on vertebrates, chiefly lizards and amphibians (Eaton, 1947; Mehrtens and Hermann, 1951; Norris and Zweifel, 1950). Babcock (1919) stated that _T. c. carolina_ has been observed to kill and eat "small brown snakes." Klimstra and Newsome (1960) recorded a racer, _Coluber constrictor_, in the diet of _T. c. carolina_, and Hutchison and Vinegar (1962) described a captive _T. c. carolina_ eating a live garter snake, _Thamnophis sirtalis_.

Material identified from 48 intestines in addition to the snake and fishes, is as follows (number of intestines in parentheses): plant material (48), stratiomyid fly larvae (39), naucorid bugs (30), curculionid beetles (22), damselfly nymphs (14), ants (13), ostracods (13), libellulid dragonfly nymphs (10), hydrobiid snails (9), hydrophilid beetles (8), isopods (5), dytiscid beetle larvae (5), gomphid dragonfly nymphs (4), belostomatid bugs (3), amphipods (3), mayfly nymphs (2), nepid bugs (2), podopid bugs (2), veliid bugs (2), chrysomelid beetle larvae (2), backswimmers (1), pentatomid bugs (1), acridid grasshoppers (1), ephydrid fly larvae (1), and bees (1).

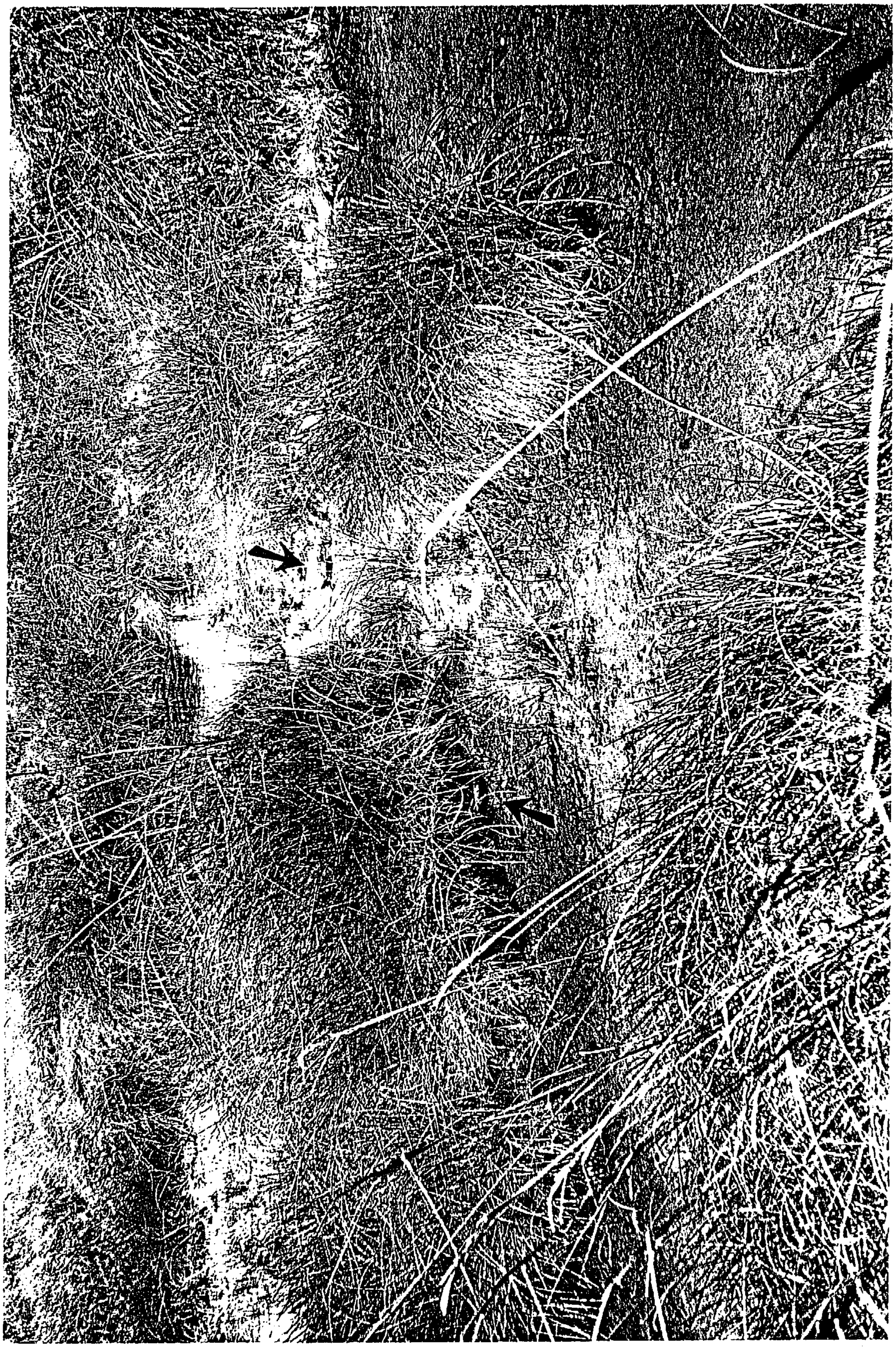
No conclusions may be reached regarding seasonal fluctuations in food habits of the Coahuilan Box Turtle due to the limited sample size and because turtles were collected only in late summer and spring. Curculionid and hydrophilid beetles were present in far greater numbers in turtles taken in July and August than in April specimens. Ants were absent in individuals taken in April, while caddisfly larvae and chaoborin midge larvae appeared more frequently in the April sample. Stratiomyid larvae occurred in more April than in July - August specimens, but made up less of the stomach volume in April. More turtles in April had eaten large quantities of Eleocharis, principally the seed heads. Intestines of four individuals were packed with several hundred Eleocharis seeds, accounting for the statement of Webb et al. (1963) cited earlier. Barton and Price (1955:161-162) examined stomach contents of 11 Bog turtles, Clemmys muhlenbergi, from Pennsylvania, finding a ". . . large number of seeds of a sedge (Carex) . . . [which were] . . . too uniformly present to be merely the result of accidental ingestion."

Stomachs in April contained slightly greater mean volumes of food material (0.98 ± 0.15 ml) than did stomachs in July and August (0.87 ± 0.12 ml), but the difference between them was not significant ($t = 0.58$; $P > 0.50$). Sampling methods also may have biased interpretations regarding seasonal variation in feeding. Of the 19 individuals in the April group, 17 were taken from a single marsh area on 4 April 1966 within a time span of about one hour. Thus, although variability exists in foods taken during any short time period by turtles living in the same restricted area, little can be said regarding the spring food habits.

No samples of organisms were taken from the environment for correlation of availability of the various food groups and the relative amounts in the diet as was done by Klimstra and Newsome (1960) in their study of Terrapene c. carolina in Illinois. They recorded over 130 different kinds of food items, with the percentage volume of the major food groups as follows: unidentified plant material (34.2%), insects (19.6%), seeds (17.4%), gastropods (10.6%), isopods (3.5%), and diplopods (2.5%). Seasonal fluctuation in numbers of Lepidoptera and Diptera larvae was accounted for by the seasonal variation in numbers of these groups, and seasonal variation in the kinds of scarab beetles was thought also to be a response to availability. In Maryland, Stickel (1950) recorded mushrooms in 43 of 60 field observations of _T. c. carolina_ feeding, with apples, millipedes, snails, caterpillars, earthworms, and beetles in the remainder. She notes, however, that the predominance of mushrooms probably occurred because most of the observations were made at times when mushrooms were abundant.

Variation in food habits of _T. coahuila_ with the habitat and among individuals is evident. The variation in kinds and numbers of food items from one turtle to another suggests that they feed on whatever is available. Five individuals were collected in relatively deep (15 - 30 cm), expansive pools near the Río Mesquites (Fig. 20). Three of these had eaten fish and were the only individuals found to contain fish from the entire sample of 48 turtles, although Williams (1960) indicated that captive Coahuilan box turtles ate fishes readily and that one individual even captured a live sunfish in shallow water. In my study, the fishes eaten were _Cyprinodon_ sp. and _Gambusia marshi_. These, and other kinds of fishes, were abundant in pools associated with the river where turtles were often seen foraging. It is possible that _T. coahuila_ caught live, quiescent fish at night by foraging along the bottom (W. L. Minckley, personal communication), or they

Figure 20. Coahuilan box turtles foraging in pools along Río Mesquites, 30 July 1965. Two turtles are indicated by arrows.



may catch fish that wander or are frightened into shallow margins. On the morning of 28 December 1964 in marshes at Posas de la Becerra (ca. 15 km southwest of Cuatro Ciénegas) a male was seen on land feeding on a dead cichlid fish, Cichlasoma sp.

On 15 July 1965 at 11:00 AM, I observed a large adult male T. coahuila feeding on Eleocharis and plant debris in shallow water of a pool along the Río Mesquites while many Gambusia and Cyprinodon swam nearly, seemingly within reach of the turtle. However, the fishes were completely ignored. In the marshes, only two (11 and N-3) regularly visited by me were inhabited by fishes. These were two species of mosquitofish, Gambusia marshi and G. longispinis in marsh 11; and G. marshi, G. longispinis, Cyprinodon sp., and Cichlasoma spp. in marsh N-3. Two turtles from marsh 11 in July 1965 were preserved and examined for food. They contained no trace of fishes. In marsh N-3, turtles were observed on several occasions from a blind constructed for that purpose. Turtles fed among beds of Chara, and, although no definite animal food items were seen to be eaten, several times turtles lunged rapidly at something in the water, possibly fishes. In this marsh on 4 April 1966 at 11:30 AM, a female foraging in water approximately 15 cm deep did not appear to notice many Gambusia marshi and Cyprinodon sp. swimming in close proximity to it. The turtle seemed to be intent on searching the mud bottom.

In an unnamed marsh visited on 24 August 1965 at 10:30 AM, an individual was foraging in shallow water while many Gambusia marshi swam to within 2 cm of the turtle's head, circling around the turtle, and apparently searching for bits of food material exposed in the mud stirred up by its activity (Fig. 21). The turtle paid no attention to the fish. Stomach contents of this individual consisted of 89% plant material (Eleocharis), an oedermerid beetle, an ostracod, and several unidentified small insects. The intestine contained plant material, stratiomyid larvae, and other insects.

Of five box turtles collected on roads, only three had food in their stomachs. The roads are adjacent to marshes, however, and in one individual the food did not differ markedly from turtles taken directly from marshes. The stomach of another contained 21 large curculionid beetles making up over 98% of the volume, and a rove beetle, the only recorded instance of this group. The third contained 39 small ants, 19 tiny limnebiid beetles, a grasshopper nymph, and a terrestrial isopod, Armadillidium vulgare. These items were probably eaten by the turtles in travelling through more terrestrial areas away from marshes.

The single individual taken from a posa (Fig. 8) in the study area was foraging on the bottom in water about 25 cm deep. This turtle was feeding among a low bed of

Figure 21. Female T. coahuila foraging in a marsh near the study area, 24 August 1965. Nine mosquitofish, Gambusia marshi, are swimming near the turtle.

Chara. It was first thought that Chara was being eaten, but the stomach contained only several small fragments of Chara along with 141 amphipods, Hyalella azteca, one sphaeromid isopod, and remains of ostracods and small snails. The tiny amphipods may represent a primary food item for which the turtle may have been searching within the Chara beds. Amphipods occurred in six stomachs of 17 T. coahuila collected on 4 April 1966 from several closely-associated marshes, but the number of amphipods in any one stomach did not exceed 14, mean 4.2. Amphipods were abundant at this time in the shallow water of the marshes and were found on the skin of box turtles when they were removed from the water. Allard (1948, 1949) noted that T. c. carolina has keen eyesight for small moving objects, but stated that tiny ants are ignored. A. V. Fitch (1965: 531), in experiments conducted with T. o. ornata, stated that ". . . live and moving food objects were more than five times as attractive as those that were motionless." Eyesight seems to play the major sensory role in the feeding of Coahuilan box turtles in nature as evidenced by their deliberate and alert actions in foraging. They can discriminate small objects, as indicated by the abundance of such items as amphipods, baetid mayfly nymphs, occasional veliid bugs, and ants. But small midge larvae, ostracods, and tiny snails are most likely eaten accidentally.

Lagler (1943) studied food habits of several species of semiaquatic of aquatic turtles in Michigan. Of four kinds of emydine turtles examined, Blanding's Turtle, Emydoidea blandingi, and the Midland Painted Turtle, Chrysemys picta marginata, show food preferences similar to Coahuilan box turtles, in that the insects eaten were primarily aquatic, immature stages of dragonflies and damselflies, and aquatic beetles and hemipterans. Insects accounted for 21.4% of the total volume of food in 66 E. blandingi examined, and 19.5% in 413 C. p. marginata. The painted turtle is more similar to T. coahuila in its extensive utilization of various kinds of aquatic plants, which made up 61.5% by volume, whereas plants were a relatively insignificant component (3.9%) in Blanding's Turtle (Lagler, 1943). Webb (1961) recorded midge larvae, ants, caddisfly larvae, and small hemipterans in stomachs of 8 Ouachita map turtles, Graptemys pseudogeographica ouachitensis, in Oklahoma, and also found a specimen ". . . gorged with grasshoppers" and one with ". . . an abundance of Bermuda grass (Cynodon dactylon) and Fogwort (Lippia incisa) in the stomach /Webb, 1961:213/." As noted earlier, the Bog Turtle, Clemmys muhlenbergi, apparently often feeds on seeds of sedges, but is also like T. coahuila in consuming insects, principally Lepidoptera larvae and beetles (Barton and Price, 1955). Data of Klimstra and Newsome (1960) for Terrapene c. carolina in Illinois (plant material 34.2%, insects 19.6%) more closely resemble the food habits of

T. coahuila than do the data for *T. o. ornata* in Kansas reported by Legler (1960). He found scarabaeid and carabid beetles, noctuid and arctiid caterpillars, and grasshoppers occurring most frequently, with all insects accounting for an average volume of 88.6% in stomachs containing them; plant material from cattle dung (in which the Ornate box turtles foraged for food) averaged 20% (Legler, 1960).

In feeding habits, the Coahuilan Box Turtle is opportunistic and omnivorous, closely resembling other aquatic or semiaquatic turtles in feeding extensively on aquatic plants and insects. The staple items in the diet are vegetative stems and seed heads of the spike-rush, *Eleocharis rostellata*; stratiomyid fly larvae, curculionid beetles, nymphs of libellulid dragonflies and agrionid damselflies, mayfly nymphs, and naucorid bugs. Isopods, spiders, and fishes appear in lesser amounts. Food preference appears to be flexible enough to allow *T. coahuila* to adjust its diet seasonally.

THERMAL RELATIONSHIPS

Methods

Cloacal temperatures of Coahuilan box turtles captured in the field were recorded with a Schultheis quick-recording mercury thermometer of the type described by Bogert (1949). After a turtle was secured, the rear half of the plastron was pried open with a thin metal blade and the thermometer inserted approximately 2 cm into the cloaca. A stable reading could be obtained within a few seconds. Even after several minuts of handling a turtle, cloacal temperature did not change noticeably and so were not apparently affected by conduction of heat from my hand to the body of the animals. Such an error was noted by Fitch (1956) in recording body temperatures of small amphibians and reptiles.

Temperatures of the environment recorded most often were: (i) water temperature at a depth of 1 to 2 cm at the site of capture (measured immediately after obtaining the cloacal temperature); (ii) air temperature measured with a dry thermometer approximately 50 cm above the substrate near the site of capture, with the thermometer bulb shaded from the sun; and, infrequently, (iii) mud substrate temperature beneath the water at the capture location.

Terminology follows Cowles and Bogert (1944) and Brattstrom (1965) for the voluntary minimum, normal activity range, preferred or optimum, and voluntary maximum temperature. The optimum body temperature is, in practice, the mean body temperature within the normal activity range, and the voluntary minimum and maximum are the lowest and highest body temperatures recorded for active animals (Brattstrom, 1965). Fitch (1956) considered the mode of a distribution of body temperatures as the optimum temperature for a given species.

I gathered 254 cloacal temperatures (and corresponding environmental temperatures) from more than 160 _T. coahuila_ in the field. The majority of records are from turtles taken in or near the study area, but those from other localities in the basin are also included.

Almost 90 percent of cloacal temperatures were accompanied by a simultaneous reading from the water in which a turtle was found. The remaining temperatures were obtained from turtles in terrestrial situations, such as roads or on dry ground at the edge of marshes. Air temperatures were recorded for turtles captured on land during July and August 1965, but were seldom obtained with turtles found in water. Air temperatures were recorded regularly in December 1965, January 1966, and April 1966.

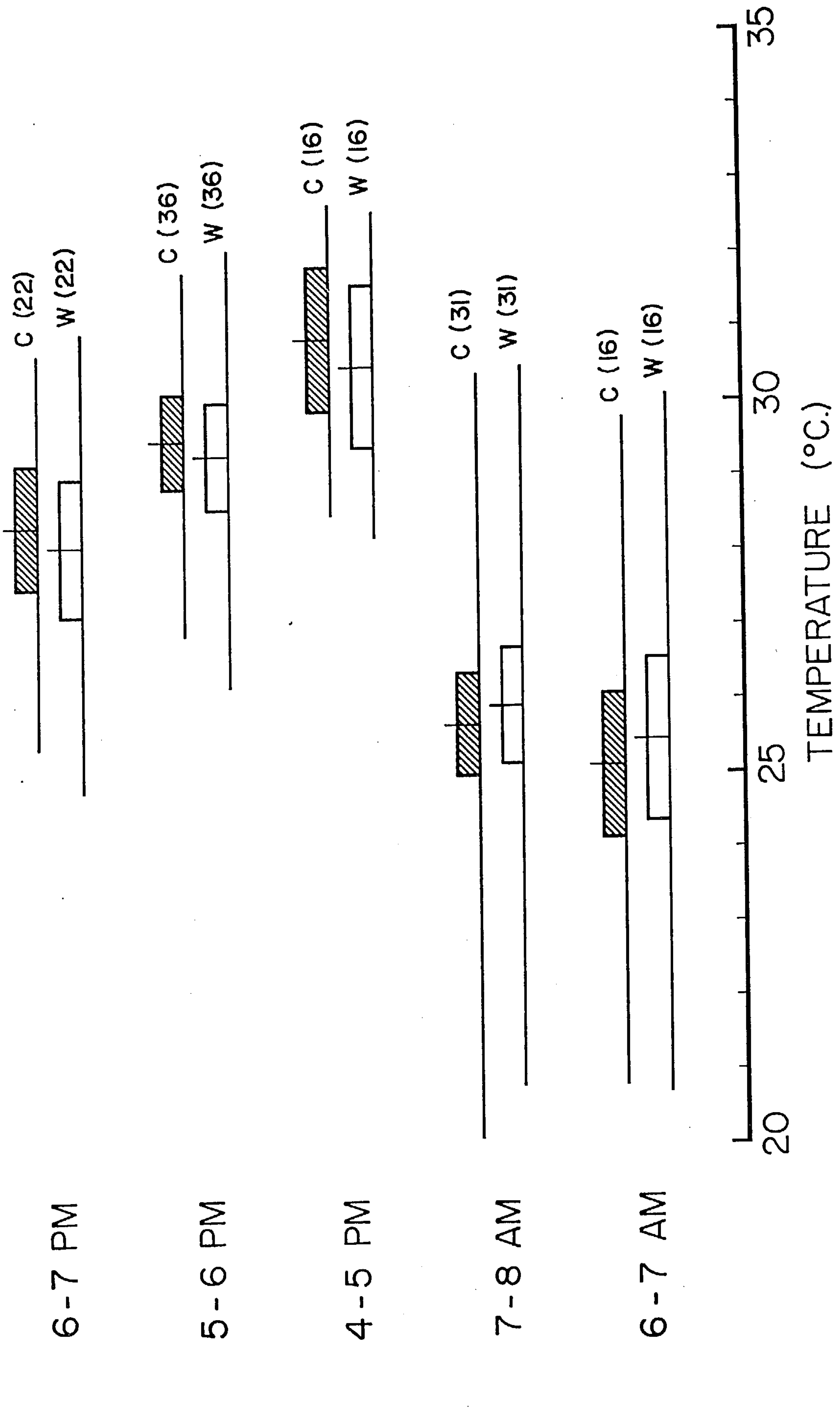
Practically all turtles were active and were observed moving or foraging for a short time prior to capture. Inactive turtles were found infrequently; they were usually in a concealed position under the base of a sedge clump, beneath mats of stonewort, or in the soft mud substrate of a marsh bottom.

Activity Temperature

Two hundred individual cloacal temperatures and corresponding water temperatures were obtained in marshes. A highly significant regression ($b = 1.01$, $P < 0.01$) exists between a turtle's body temperature and that of the water in which it was active. Brattstrom (1965) and Edgren and Edgren (1955) reported body temperatures of *Sternothaerus odoratus* closely approximating the surrounding water, and Boyer (1965) noted body temperatures of aquatic turtles in water were nearly identical to water temperatures. Body temperatures of *Chrysemys picta* in early spring were near those of the water, but several turtles were able to raise their body temperatures as much as 2 C, apparently by absorbing solar radiation (Sexton, 1959b).

Of 121 *T. coahuila* caught in marshes in July and August 1965, 114 had cloacal temperatures slightly different from water temperatures. Approximately half the temperatures varied from 0.1 to 1.7 C greater than water, and about half had an identical range below the water temperature. A trend for cloacal temperatures to be slightly lower than the surrounding water in the morning was apparent, but during the afternoon most individuals were warmer than the medium (Fig. 22). Only 21% of 45 turtles between 6:00 and 8:00 AM had

Figure 22. Daily fluctuation in water (W) and cloacal (C) temperatures of <u>T. coahuila</u> active in marshes during July and August 1965. Vertical and horizontal lines represent mean and range of observed variation, respectively. Blocks represent 95% confidence limits; number of records for each hourly period are in parentheses.


6-7 PM
5-6 PM
4-5 PM
7-8 AM
6-7 AM
C (22)
W (22)
C (36)
W (36)
C (16)
W (16)
C (31)
W (31)
C (16)
W (16)
20
25
30
35
TEMPERATURE (°C.)

cloacal temperatures higher than water, whereas between 4:00 and 7:00 PM, 64% of 69 turtles had temperatures above that of the water. This may result from the more intense afternoon sunlight and an increasing heating effect of light waves as the angle of incidence becomes greater. Boyer (1965) found angle of incident light to be a factor in increasing heat gains of turtle models, and noted that turtles of the genus Pseudemys orient while basking to receive maximum heat absorption through a more direct angle of incidence. Almost all Coahuilan box turtles active in marshes were in shallow water, with the carapace dry and exposed directly to sunlight.

During both December 1965 and April 1965 and 1966, approximately two-thirds of the cloacal temperatures were higher than water temperature, differences ranging from 0.2 to 1.3 C in December and from 0.1 to 3.4 in April. The mean cloacal temperature in December does not reflect this trend, however, being slightly less than the mean water temperature (Fig. 23). In several instances turtles that had recently emerged from deep in the mud substrate had body temperatures as much as 3.3° lower than surface water temperatures, thereby lowering the mean. The same situation obtained in January 1966, when temperatures in 9 of 10 turtles varied from 0.1 to 3.0 C below that of surrounding water. A number of the individuals were captured while emerging from beneath the mud and thus had lower cloacal temperatures. Three emerging _T_. _coahuila_ had cloacal temperatures 2.7, 2.9, and 3.0 C below that of the surface water.

Although cool, all days in the field during December 1965 were clear and summy; air temperatures averaged 17.6 C. In contrast, three of the four days on which turtles were captured in January 1966 were overcast, and the air averaged 11.1 C. Some differences between temperature data from these two winter months are, therefore, accountable. Active turtles, with carapaces exposed to air, probably are affected by low air temperatures, and clouds can effectively reduce insolation and rates of heat gain (Boyer, 1965).

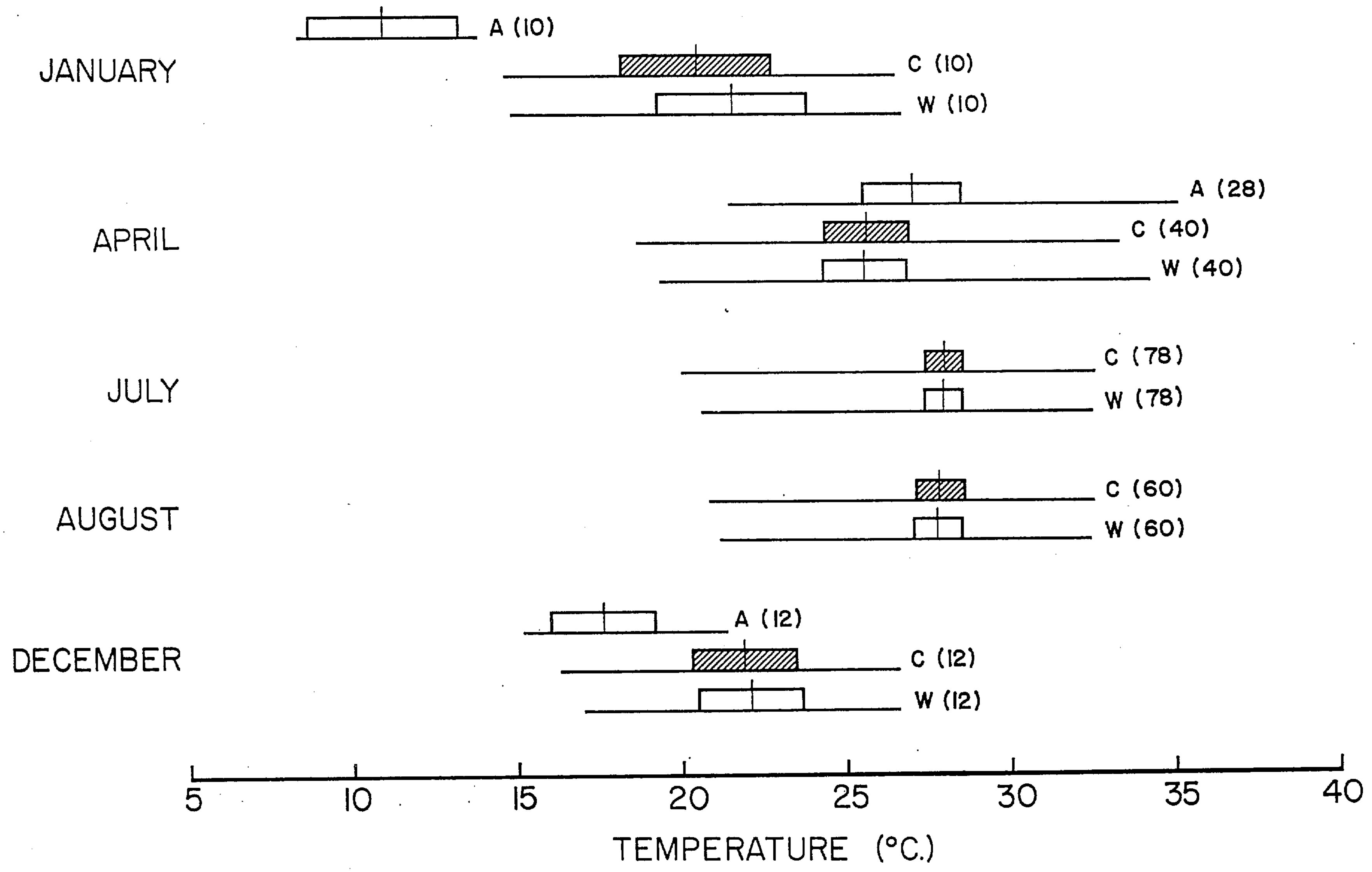
Seasonal variation in the normal activity range of _T_. _coahuila_ in marshes is evident in Table 11 and Figure 23 . Cloacal temperatures in December and January are significantly lower than those in April, and the last differ significantly from records in July and August. Mean cloacal temperatures during winter months are about 21.0 to 22.0 C, varying from 14.8 to 26.7 C. In spring (April), mean cloacal temperature is near 26.0 C, and during the summer months (July and August) the mean rises to 28.0 C.

With data presently available, showing such wide seasonal fluctuations in the mean body temperature, it is doubtful that a meaningful optimum or preferred body temperature can be given for _T_. _coahuila_. A voluntary minimum temperature of 14.8 C (January) and a voluntary maximum of 33.5 (April) were the extreme body temperatures recorded at

Table 11. Water and cloacal temperatures of *Terrapene coahuila* in marshes during five months of the year, and during five hours of the day in July and August 1965. Number of records in parentheses.

Month	Water		Cloaca	
	Mean ± 1 SE	Extremes	Mean ± 1 SE	Extremes
July (78)	28.08 ± 0.30	20.7 - 32.6	28.14 ± 0.30	20.1 - 32.7
August (60)	27.84 ± 0.38	21.2 - 32.5	27.94 ± 0.38	20.9 - 32.6
December (12)	22.08 ± 0.79	17.0 - 26.6	21.93 ± 0.79	16.3 - 26.6
January (10)	21.75 ± 1.12	15.0 - 26.9	20.67 ± 1.12	14.8 - 26.7
April (40)	25.74 ± 0.65	19.5 - 34.4	25.80 ± 0.65	18.8 - 33.5
Hour				
6 - 7 AM (16)	25.47 ± 0.56	20.7 - 30.1	25.12 ± 0.49	20.8 - 29.8
7 - 8 AM (31)	25.93 ± 0.40	20.8 - 30.5	25.68 ± 0.36	20.1 - 30.4
4 - 5 PM (16)	30.51 ± 0.56	28.2 - 32.6	30.88 ± 0.49	28.5 - 32.7
5 - 6 PM (36)	29.33 ± 0.37	26.2 - 32.1	29.53 ± 0.33	26.9 - 31.8
6 - 7 PM (22)	28.12 ± 0.47	24.8 - 31.0	28.39 ± 0.42	25.4 - 30.7

Figure 23. Seasonal variation in cloacal (C) temperatures of *T. coahuila* active in marshes during five months of year, showing relationship with water (W) and air (A) temperatures recorded at times of capture. Vertical and horizontal lines represent mean and range of observed variation, respectively. Blocks represent 95% confidence limits. Number of records in parentheses.


JANUARY
A (10)
C (10)
W (10)
APRIL
A (28)
C (40)
W (40)
JULY
C (78)
W (78)
AUGUST
C (60)
W (60)
DECEMBER
A (12)
C (12)
W (12)
5
10
15
20
25
30
35
40
TEMPERATURE (°C.)

all seasons within marshes, and these give the approximate limits of the normal activity range in shallow water. Fluctuations in cloacal temperatures follow closely the seasonal changes in water temperature of the marshes brought about by over-all climatic changes of the area. The mean monthly air temperatures for Cuatro Ciénegas presented by Contreras (1942) show December and January as the coldest months, to July and August as the hottest, with April intermediate between the two. *T. coahuila* is apparently a thigmotherm in its marsh habitat where it corresponds, in part, with other aquatic forms ". . . that derive their effective body temperatures solely from the medium in which they live" (Cowles, 1962:670).

During July and August 1965, when most data were taken, records were divided into one-hour periods to test variation in cloacal temperatures due to time of day (Fig. 22). There is a highly significant difference ($F = 33.2$, $P < 0.01$) in mean cloacal temperatures between the time periods. Cloacal and water temperatures were lowest between 6:00 and 7:00 AM (mean cloacal 25.1, range 20.8 - 29.8 C), the period shortly after sunrise, before insolation had an opportunity to raise water or cloacal temperatures. Maxima for the time periods indicated were attained between 4:00 and 5:00 PM (mean cloacal 30.9, range 28.5 - 32.7 C). Seventeen temperature records obtained at other times during the day were as follows (mean water temperatures, followed by mean cloacal temperature, and number of records in parentheses): 8:00 - 9:00 AM: 24.0, 24.3 (3); 9:00 - 10:00 AM: 28.6, 28.6 (3); 10:00 - 11:00 AM: 27.8, 27.8 (1); 11:00 - 12:00 AM: 32.0, 32.3 (2); 12:00 - 1:00 PM: 31.9, 32.7 (2); 1:00 - 2:00 PM: 29.8, 31.1 (2); 2:00 - 4:00 PM: no data; and 7:00 - 8:00 PM: 28.1, 28.0 (4).

The few records available for mid-day are highest of all cloacal temperatures recorded from turtles within marshes. The lack of records during these intervals reflects, in part, a cessation of field work, but box turtle activity was also at its lowest level in that period.

Mean cloacal temperatures slightly lower than surrounding water temperatures in morning hours, and higher than water in afternoon, may indicate a lag of cloacal temperatures in comparison to progressively increasing, or decreasing, temperatures of the water through the day. Baldwin (1925) recorded a lag in cloacal temperatures of 1.5 to 3.0 C when aquatic turtles of several species were exposed to changing water temperatures.

In T. coahuila, a greater range of variation in both cloacal temperatures and water in morning than in the afternoon (Fig. 22) results from more variable microclimatic conditions in marshes in the former period, and from records of turtles at widely-varied stages of warming.

Ten body temperatures were taken from turtles collected incidentally from pools of the Río Mesquites in July and August 1965. All were recorded in late morning or early afternoon, and temperatures of both water and cloacae were high. Water temperatures ranged from 28.7 to 33.7 C, and corresponding cloacal temperatures ranged from 28.5 to 33.6 C. At 2:40 PM on 30 July 1965, with the mountains obscured by haze and the sun hidden, five turtles were collected from this habitat (Fig. 20). Despite the cloud cover, water temperatures were near 33.0 C; cloacal temperatures of the turtles were unusually high, ranging from 31.4 to 33.6 C.

Posas (large sinkholes) in the study area are generally fed by thermal springs and have the highest water temperatures of all aquatic habitats sampled. Two posas, providing water to marshes 3 and 11, ranged from 30.9 C in January 1966 to 34.7 C in October 1966 for the posa of marsh 3 (mean of six records, 32.1 C), and from 32.8 C in January 1966 to 34.2 C in July 1966 for the posa of marsh 11 (mean of six records, 33.5 C). Temperatures in these habitats are probably always above 30.0 C, regardless of the time of year. On 31 July 1965, a female had a cloacal temperature of 34.1 C in posa 11 (water 34.0 C), the highest voluntary body temperature of any T. coahuila recorded while in water. Two other body temperatures of turtles in posas were 33.4 C and 32.1 C, recorded in August 1965. Both were 0.1° above the water temperature. A fourth individual was seen in posa 11 on 14 October 1966 in water 34.0 C, but was not caught. The posa of marsh 9 is apparently not fed by warm spring water; its temperature ranged from 19.4 C in January 1966 to 31.7 C in July 1966 (mean 23.9 C for 5 samples). No box turtles have been observed in this pool.

T. coahuila on sedge tussocks within marshes, at the edge of a marsh, or in the grassy terrain away from water provided unique temperature data and an opportunity to observe the effects of an uncommon thermal environment. Boyer (1965) points out that substratum temperatures can be important in affecting body temperatures, but that it remains unclear whether the close relation between substrate temperature and the body temperature of the animals ". . . is a result of common factors (i.e., insolation and air temperature) or whether body temperature is the result of substrate temperature [Boyer, 1965:106]." However, he notes that during the warmer parts of the year, a turtle will usually gain heat merely by emerging from the water since ". . . air temperatures above water and ground tend to be much higher than those of the substrate, especially in daytime" (Boyer, 1965:107). A female T. coahuila on 6 July 1965 at 6:15 AM on a dry sedge clump in marsh 2, had a cloacal temperature of 20.3 C (air 21.4 C); her lower temperature presumably reflects the cool soil beneath her. Another female at the edge of this marsh the previous day at 6:30 AM had a cloacal temperature of 21.8 C (air 23.5 C). On 4 August 1965, however, at 6:25 AM, a female was found resting in a horse path approximately 100 m south of marsh

11. Cloacal temperature was 22.4 C. The air temperature was 21.1 C, and the morning was cloudy, cool, and damp, with a brisk easterly breeze blowing. On the afternoon of another overcast day, 12 July 1965, a turtle caught in grass near a marsh, in shade and on a cool substrate, had a body temperature of 28.8 C (air 31.6 C).

The last two observations point out that Coahuilan box turtles are sometimes active away from the marshes in summer under overcast skies. Movements of box turtles on sunny days across unprotected, open areas, may be restricted to morning hours before mid-day temperatures reach critical levels, at least in summer. Four turtles encountered on roads between 6:05 and 8:40 AM during July and August 1965 had cloacal temperatures ranging from 23.2 to 28.6 C (mean 25.3 C). Air temperatures were 1.8° and 2.5° greater than cloacal temperatures the two times they were recorded.

The highest cloacal temperature recorded during this study was 34.5 C from a male on 23 August 1965 at 5:25 PM in grass about 50 m from the nearest marsh. The weather was clear, air temperature 32.9 C. This body temperature was approaching the upper critical voluntary thermal level for the species (see below).

Although Heath (1964) has stressed that thermoregulation cannot be definitely ascribed to an animal whose activities prior to measurement are not fully known, field evidence indicates that _T. coahuila_ does exhibit basking behavior. The most convincting data for elevation of body temperatures by basking were obtained in winter, on 21 December 1965. Air temperatures at mid-day varied between 17.0 and 19.1 C under a clear, sunny sky with a moderate southerly breeze. The body temperature of a turtle in marsh 6 at noon was 24.6 C in water of 23.8 C. Several minutes later, a second individual with a body temperature of 33.1 C, was discovered on land at the edge of the marsh. This was more than 14.0° above the air temperature. A half hour later in marsh 3, an individual with a cloacal temperature of 20.8 C was in water of 19.5 C. Nearby in the same marsh, but on a dry tussock of sedge, another turtle had a body temperature of 28.8 C, 11.8° higher than the air. Later the same day, a third turtle on land had a cloacal temperature 6.5° above that of the air. The mean difference between cloacal and air temperatures for these three turtles was 10.8 C. Their mean body temperature was 29.2 C, while three other individuals in water at the same time had body temperatures 5.0 to 9.0° lower, corresponding to the water temperatures.

In April 1965 and 1966, mean air temperature at times of turtle captures was 27.2 C; slightly, but not significantly, greater than marsh water temperatures (Fig. 23). All but two of six days during April 1966 were sunny and clear, probably contributing to the mean cloacal temperature slightly above mean water temperature. On the morning of 7

April 1966, three of five turtles captured had cloacal temperatures from 0.2 to 1.7° higher than the water, presumably through absorption of incident energy, despite a completely overcast sky and light precipitation.

Data obtained in summer, like those from April, are less strongly indicative of basking, but appear pertinent. Cloacal temperatures of box turtles on a dry substrate in summer were raised at most only 2.4° above air temperatures. On 31 July 1965, at 8:05 AM, a female was on dry ground at the edge of marsh 5. Cloacal temperature was 25.3 C, 2.1° above the air temperature (23.2 C). The morning was hazy, with a slight easterly breeze. The turtle appeared to be in early stages of basking. Two days later, on 2 August 1965, again with the weather hazy and with a slight easterly breeze, two turtles were found on land. Their body temperatures were near prevailing air temperatures, which were high. The first, at 10:10 AM, had a cloacal temperature of 31.9 C (air 34.3 C), and the other at 10:35 AM registered 33.3 C (air 32.9 C). These observations further indicate that Coahuilan box turtles are capable of achieving elevated body temperatures, even under overcast skies. Boyer (1965) has found this to be true for other species of turtles, and that light from an overcast sky is capable of elevating the temperature of an artificial black body to 1.0 to 3.0 C above air temperatures.

The rates of change in body temperature of T. coahuila, and levels of heating attained while basking, appear similar to those reported for other species. Cagle (1946) placed individual Pseudemys scripta elegans in direct sunlight and found body temperatures rising as much as 11.0 C above air temperatures in slightly more than 2.5 hours. Mean body temperature of 30.6 C for the same species basking in the laboratory, and body temperatures of 35.8 C and 37.9 C for basking Chrysemys picta when air temperatures varied from 20.0 to 30.0 C and water from 22.0 to 28.0 C, were recorded by Boyer (1965). Brattstrom (1965) gave a mean body temperature of 27.8 C for seven basking C. picta; six others active in water had a mean of only 14.0 C. Sexton (1959b) reports C. picta sunning on shore in early spring capable of raising their body temperatures far above air temperatures (8.0°, 11.5°, 12.0°, and 16.8° higher in four individuals). Legler (1960) gave a mean body temperature of 60 basking Terrapene o. ornata as 25.5 C (range, 17.3 - 31.4 C). Basking occurred between sunrise and 11:00 AM, with more than two-thirds of the body temperatures taken in that period ranging higher than air temperatures.

Boyer (1965:103) considered it ". . . probable that body temperatures achieved by basking animals are frequently . . . not far from lethal . . . ." On 15 July 1965, I performed a crude experiment in the field using an adult female T. coahuila to determine the approximate upper limit of temperature tolerance. At 1:36 PM, under direct sunlight, the turtle was tethered on a string about 1.5 m long on the rocky slope at the study area. After 16 minutes, at a cloacal temperature of 36.6 C, the plastral muscles contracted weakly and the turtle did not completely close its shell when disturbed; at 37.5 C, after 22 minutes, it made almost no attempt to close the shell; death seemed imminent. Gaping and frothing at the mouth, presumably to cool the body by evaporation, appeared early in the experiment. Distress and frantic efforts to reach nearby shade were evident after seven minutes, after the body had reached approximately 35.0 C. This probably represents the maximum temperature tolerated by T. coahuila in nature (the highest body temperature recorded in the field was 34.5 C). A similar upper limit was reported for T. o. ornata in Kansas by Legler (1960:603), who states: ". . . ornate box turtles do not often tolerate body temperatures above 33 degrees and . . . temperatures in excess of 35 degrees are probably never tolerated under natural conditions." Legler thought 40.0 C represents the approximate lethal temperature for T. o. ornata. Although I conducted no experiments to determine the critical thermal maximum (CTM) of T. coahuila, body temperatures near 40.0 C in all likelihood approach the lethal level. Hutchison et al. (1966) report CTMs ranging from 42.5 to 43.0 C in T. carolina, and give a mean CTM of 41.6 C in the semiaquatic emydines.

Daily and Seasonal Activity

In the summer of 1965, Coahuilan box turtles were active from shortly after sunrise (about 6:00 AM) until several hours after dark (10:00 PM). Cloacal temperatures of turtles between 6:00 and 7:00 AM ranged from 20.8 to 29.8 C (mean 25.1 C). Air temperatures in this period averaged 21.7 C (range 16.7 - 25.6 C, 34 records). Air temperatures were recorded in the study area between 6 July and 9 August 1965 with two maximum-minimum thermometers placed about 50 cm above the water surface in marshes 3, 5, and 11. Maximum air temperatures ranged from 31.7 to 40.0 C (mean of 47 records, 36.0 C). Minimum air temperatures came in the early morning hours, before daylight, ranging from 15.6 to 22.8 C (mean of 49 records, 19.3 C). Environmental temperatures (air and water) increased to a maximum at mid-day or early afternoon. In this period, few box turtles were active.

Legler (1960) noted that most T. o. ornata in Kansas remained inactive in mid-day hours on hot summer days, and Penn and Pottharst (1940) observed morning and later afternoon periods of activity in summer for T. c. major in Louisiana. The time between was spent in "diurnally periodic" dormancy. I found two T. coahuila on 11 July 1965 at 12:15 PM under the thick cover of a composite shrub and sedges, at the edge of marsh 6. Air temperature was 34.4 C, and cloacal temperatures of the turtles were 29.1 C and 29.5 C; shallow water beneath the plant cover was 28.6 C. This retreat appeared to be in regular use, as it had a well-defined depression in the mud. Two days later, a third individual was in this place at 5:00 PM. Cloacal temperature was 29.2 C, and water 28.9 C.

Water temperatures during summer at mid-day are often above tolerable levels for T. coahuila. High water temperatures in the study area were recorded on 25 July 1966 between 12:30 and 1:45 PM (Table 12). The day was clear and hot, despite a brisk easterly wind. Air temperature was 35.0 C. Water temperatures of 37.8 C in marsh 6 and 35.3 C in marsh 2-A were recorded. On 14 October 1966 at 1:15 PM, a temperature of 38.8 C was attained by open water in marsh 8. Such maximums are certainly not tolerated by T. coahuila, and no box turtles were found in the marshes where they were recorded. Just 5 or 6 cm below the water surface, temperatures of mud bottoms were approximately 5.0° cooler than water. Mud temperatures drop steadily with depth, providing a cool refuge into which a turtle can readily retreat by burrowing, to avoid potentially harmful temperatures of the shallow waters above.

In addition to avoidance of high temperatures on summer days, Coahuilan box turtles seem to alternate periods of activity with periods of rest. One male T. coahuila remained in uninterrupted quiescense for nearly four days. I recorded the turtle at 7:35 AM on 20 July 1965 in marsh 10, and watched it dig into the base of a sedge clump. The

Table 12. Water and mud temperatures in marshes on 25 July 1966, 12:30 - 1:45 PM.

Marsh	Water Temperature	Mud Temperature
2-A	35.3	29.1
2	32.6	30.0
5	34.8	29.2
6	37.8	32.0
9	36.2	----
3	37.5	----
9	34.5	----
11	36.5	----
	$\bar{x}$ = 35.65	$\bar{x}$ = 30.07

form was checked each morning and evening of the following days to verify the presence of the turtle. It remained there, well-covered by vegetation and in shallow water, until the night of 23 July or the early morning of 24 July. A distinct depression, covered by plant material, was left. Resting for several days and then resuming activity was a conspicuous feature of *T. c. carolina* behavior in Maryland (Stickel, 1950), and Legler (1960) noted that some *T. o. ornata* in Kansas were steadily quiet for several consecutive days during summer.

Unlike other box turtles, *T. coahuila* is to some extent nocturnal, although Webb et al. (1963:96), observing that *T. coahuila* is crepuscular, stated: "Captive individuals . . . could not be induced to move, even by offering food, in darkness." Marshes in the study area were visited on three nights in the summer of 1965, and on two occasions active box turtles were found. On 5 July, between 9:45 and 10:00 PM, two individuals were foraging in shallow water of marsh 5. Cloacal temperatures were 23.5 C and 24.4 C, in water of 23.3 C. On 18 July at 8:50 PM in marsh 2, an individual was active with a cloacal temperature of 27.0 C, in water of the same temperature. An hour later, a second turtle in marsh 8-A had a cloacal temperature of 27.4 C in water of 27.8 C. All individuals appeared to be foraging in the same manner as during the day. No turtles were sighted between 11:30 PM and midnight on 3 August 1965.

Breder (1927), Allard (1935), Cahn (1937), and Stickel (1950) reported a lack of nocturnal activity in *T. c. carolina*. Legler (1960) showed by the use of thread trails that the activity of *T. o. ornata* ended at dusk, but Brattstrom (1965) apparently overlooked Legler's findings and relied on a speculation by Fitch (1956) that the activity of *T. o. ornata* in hot summer weather seemed to be nocturnal.

Winter activities of *T. coahuila*, except in thermal springs and marshes, may be curtailed by low water temperatures. On 28 December 1964 at Posas de la Becerra, 15 km southwest of Cuatro Ciénegas, seven *T. coahuila* were found in shallow (ca. 20 cm) water of a series of large marsh pools. Air temperatures ranged from 10.0 to 15.0 C, and water from 7.2 to 16.5 C, from about 8:00 to 11:00 AM. The box turtles were inert when discovered, mostly buried in the flocculent bottom material. Body temperatures ranged from 7.2 to 12.4 C, mean 10.0 C. In the study area, *T. coahuila* that had body temperatures lower than 14.8 C were not found in December 1965 and January 1966. Webb et al. (1963:96) noted that the activity of captive *T. coahuila* ". . . was markedly reduced at 60°F [15.6 C], and they seemed torpid at temperatures below 50°F [10.0 C]." Legler (1960) found no *T. o. ornata* active at temperatures below 15.0 C, and *Chrysemys picta* in Michigan apparently do not begin to feed actively until water temperatures are above 15 C (Sexton, 1959b).

I performed a laboratory experiment with six adult _T. coahuila_ of both sexes to determine the approximate lower temperature limit that can be tolerated before body movements are impaired. Turtles were placed in a water bath of crushed ice at 0 C. When completely torpid, they were removed and placed on a dry surface at room temperature and allowed to warm slowly. Cloacal temperatures were recorded at the first successful forward movement that was accomplished with limb control and limited power of locomotion. Body temperatures when first movements occurred ranged from 6.0 to 16.4 C in 12 trials. All temperatures except the extremes were in the range 10.2 to 14.4 C, and the mode was 12.0 C (mean 12.2 C). These observations indicate the minimum effective temperature for movement in _T. coahuila_ as approximately 12.0 C. The minimum temperature tolerated voluntarily is probably 14.0 to 15.0 C.

Mean monthly temperatures recorded at Cuatro Ciénegas for November, December, January, and February are 19.0, 14.6, 13.6, and 17.4 C, respectively (Contreras, 1942). For 1965, mean temperatures for these months were 18.5, 13.2, 14.1, and 13.0 C, and a mean of 16.6 C was recorded for March (Modesto de la Garza P., personal communication). Most years, mean monthly air temperatures would, therefore, fall below the probable average minimum temperature of activity for _T. coahuila_ (approximately 20.0

C) in the five month period November through March. Average maximum temperatures for any month of the year do not fall below 20.7 C (December and January), however, and absolute maximums recorded for these months were 36.5 and 33.0 C (Contreras, 1942). Records of 25.0 C and 28.0 C as absolute maximums are available for December and January 1965. The number of days reaching a maximum temperature greater than 20 C in December 1965 was 10, and there were four in January 1966 (Modesto de la Garza P., personal communication). Cloacal temperatures of 12 active box turtles recorded in the study area between 20 and 22 December 1956 (10:30 AM - 2:35 PM) averaged 21.9 C, and 10 between 24 and 28 January 1966 (10:45 AM - 12:35 PM) averaged 20.6 C. Ambient water temperatures averaged slightly greater (22.1 and 21.8 C). None of these records was on a day when maximum air temperatures recorded by De la Garza reached 20.0 C or higher. Air temperatures at the study area, recorded at the times of capture, ranged from 15.2 to 21.4 C (mean 17.6 C) in December, and from 8.5 to 14.0 C (mean 11.1 C) in January, significantly below both water and cloacal temperatures. On winter days, despite low air temperatures, box turtles are often active.

Diurnal activity follows ambient water temperatures more closely than air temperatures, but many nights in December, January, and February are cold (air 0 C or below). Although I recorded no evening water temperatures from the marshes in winter, Contreras (1942) gives average minimum air temperatures of 9.0, 7.6, and 9.9 C, and extreme minimums of -2.0, -0.3, and -1.0 C, respectively, for these months. Such low air temperatures would drive surface water temperatures below that voluntarily tolerated by box turtles, forcing them into the mud bottom of marshes where temperatures would likely be more favorable. Many members of the population are active in the daytime throughout the year, but nearly all turtles may undergo temporary states of inactivity at night to avoid the cold, especially from December through February.

MOVEMENTS

The distance between successive sites of capture was measured in 54 of 162 movements (33%) of 61 recaptured <u>T. coahuila</u> over the entire study area. Considering only the main study area of 11 marshes, 48 of 140 (34%) of the recorded movements of 52 recaptured individuals were measured. A few distances were paced in the field, but most were measured on outline maps of the marshes as a straight-line distance between the two successive points of capture. Field distances were recorded to the nearest meter and map distances to the nearest half meter. There were no apparent differences between distances traveled within marshes in the main study area and those in outlying marshes.

Table 13 gives distances traversed by <u>T. coahuila</u> within and between marshes; 76% of recorded movements were within the marsh where the animal was previously marked, and 61% were by females. The mean distance between successive points of capture for 14 movements of males in the same marsh was 15.0 m, and for 27 movements of females, 11.7 m. Since the difference is not significant ($t = 0.90$, $P > 0.30$), movements of the sexes were combined to obtain a mean straight-line distance of 12.8 m between successive points of capture for 41 movements of 31 individuals within marshes.

Table 13. Movements of *Terrapene coahuila* in the study area. Measurements are mean straight-line distances in meters between successive points of capture; ranges in parentheses.

	Within Marsh	Between Marshes
Males	n = 14	n = 7
	15.0 (3.0 - 50.0)	84.6 (23.0 - 250.0)
Females	n = 27	n = 6
	11.7 (2.5 - 51.0)	62.1 (20.5 - 140.0)
Both Sexes Combined	n = 41	n = 13
	12.8 (3.0 - 51.0)	74.2 (20.5 - 250.0)

Although the sample is not as large as might be desired, the measurements can be used to estimate the size of the area over which a turtle habitually travels, or its home range. The data are not sufficient, however, to permit such refined home range calculations as the center of activity or the mean recapture radius (Hayne, 1949a; Tinkle and Woodward, 1967), or even for mapping minimum home ranges by the minimum polygon method (Hayne, 1949a), since a maximum of four movements was recorded for only two individuals, and two movements for four individuals. An acceptable, though less accurate, substitute was used by Legler (1960) to calculate home range size in T. o. ornata. The average distance between successive points of capture was assumed to represent the radius of the home range. The area of the home range of 44 T. o. ornata computed by this method differed only slightly from the area of eight individuals with enough recapture records to allow actual measurement (Legler, 1960).

Considering 12.8 m as the average home range radius of T. coahuila, the mean diameter is 25.6 m. One factor that may affect this size, however, is the size of the marsh in which a turtle was recorded; movements within a marsh would necessarily be restricted by its dimensions. Straight-line movements of 10 individuals in the two smallest marshes (6 and 1) ranged from 3.5 to 15.0 m, mean 8.2 m. In the two largest marshes (3 and 11), 15 movements ranged from 4.0 to

28.0 m, mean 13.6 m. It is possible for turtles to travel 50 to 130 m from opposite ends of the long (north-south) axes in the last marshes, but the close similarity of distances moved indicates that Coahuilan box turtles in the study area utilize areas of roughly equal size regardless of the size of the marsh. Another factor possibly affecting an estimate of home range size is the time elapsed between captures, with shorter distances correlated with shorter time intervals, and vice versa. However, there was no indication of such a correlation in _T. coahuila_. Lengths of time between captures within the same marsh ranged from 1 to 464 days; 61% of the intervals were less than 50 days and the mean distance of movement of these turtles was 10.5 m. Of those animals (n = 16) free for more than 50 days after marking (average of 214 days), the mean distance was 16.4 m. Stickel (1950) reported no correlation between the distance traveled and the time elapsed between collections of _T. c. carolina_.

Several estimates of home range size have been made for species of _Terrapene_. Stickel (1950) calculated the maximum distance between the two farthest points of capture for 55 _T. c. carolina_ in Maryland during one season; the average maximum diameter of the home range was 100.6 m for males and 112.8 m for females. In New York, Nichols (1939c) recaptured 12 _T. c. carolina_ 45 to 228 m from their original capture points after one month to six years. The mean distance between successive points of capture was 118.9 m.

Based on 291 captures over three years, the mean distance between successive points of capture of T. c. carolina in Indiana was 69.5 m (an average home range diameter of 139 m) (Williams, 1961). Williams (1961) also calculated home range size for 130 recaptured individuals by measuring the maximum distance between the two farthest captures. The result was 114.2 m, a mean home range diameter similar to that reported by Stickel (1950). T. c. triunguis in Oklahoma often move from one hibernaculum to another in the same or different year (Carpenter, 1957). Distances between successive hibernacula were viewed by Carpenter (1957:282) to be ". . . related to the size of the activity range of this species." Mean distance between successive hibernacula in successive years for 60 turtles was 49.4 m, and in the same year for 45 turtles, 51.2 m. If these distances are considered as radii, the approximate home range diameter is 100 m in the T. c. triunguis population. Distances between 146 captures of 44 T. o. ornata in Kansas ranged from 22 to 278 m, mean 84.8 m; the mean home range diameter, then, becomes 166.5 m (Legler, 1960).

T. coahuila forage in shallow water, following networks of small rivulets through mats of Chara and around the base of Eleocharis clumps. A web-like system of water courses is evident in most of the Cuatro Ciénegas marshes, especially through stonewort. These trails are kept open by foraging box turtles and their activities may help to maintain a flow of water throughout a marsh. Coahuilan box turtles seldom move in a direct line, but change directions, double back, and turn frequently, following the reticulated design of rivulets within the marsh vegetation. The straight-line distances between points of collection, therefore, do not represent the actual pattern of movement of the animals, except in a very general way.

The Bog Turtle, *Clemmys muhlenbergi*, in northeastern USA, inhabits *Sphagnum* moss - *Carex* sedge marshes similar in formation to the *Chara* - *Eleocharis* marsh habitat of *T. coahuila*. Barton and Price (1955:160), in describing the *C. muhlenbergi* habitat and the turtles, state: "The intersecting rivulets cut their ways through the blanket of moss, and provide the runways along which the bogturtle roams." Barton and Price (1955:161) commented further: "The bog-turtle is rather a frequenter of shallow meandering water courses; its domed shell is only occasionally wet, but its feet are nearly never dry." Sexton (1959b) described foraging actions of *Chrysemys picta* on mats of surface vegetation in a pond. The turtles generally moved with their carapaces above the water surface and their heads extended forward beneath the water. They used ". . . exploratory strikes of the head into vegetation to disturb potential prey . . ." (Sexton, 1959b:133). Patterns of foraging of these two species are notably like those of *T. coahuila* (see "Foraging Behavior"). *T. coahuila* appears, on this basis, to be as well-adapted to its mode of life as do these, and possibly other, aquatic emydines.

All marshes in the main study area are oriented in a northeast-southwest direction (Fig. 7) and it is not surprising that 20 of 25 turtle movements within marshes were either northeast or southwest, following the long axis of a marsh. Five of 25 were in the opposite directions, northwest or southeast. Nine of 14 movements were recorded as directly north or south; only five were east or west.

No aggressive encounters between Coahuilan box turtles were observed in the field. Frequently, individuals were foraging within several meters of other turtles without taking special notice of them. I have no evidence that there is active defense of a territory in nature. However, frequent fights between Coahuilan box turtles have been observed under semi-natural conditions in an outdoor enclosure at Arizona State University (W. L. Minckley, unpublished data). Fighting between _T. coahuila_ in nature may not be as rare as suggested, but may only be difficult to observe as has been pointed out by Evans (1961). Evans (1956a, 1956b) reported aggressiveness and social hierarchies in captive _T. c. carolina_, and Penn and Pottharst (1940) reported marked aggressiveness and fights among captive _T. c. major_. In the lengthy field studies on _T. c. carolina_ (Stickel, 1950) and on _T. o. ornata_ (Legler, 1960), no definite instances of fighting were observed.

Most _T. coahuila_ are rather sedentary, tending to remain within a given marsh for relatively long periods (Table 14). However, 11 of 52 (21%) recaptured turtles in the main study area moved from one marsh to another 13 times. Most of the distances traveled were less than 100 m, and the mean was 74.2 m (Table 13). Some inter-marsh travels, if direct, were made across stretches of barren ground. These areas could be crossed only at times of day when temperatures would permit, as in the early morning or late evening. A female was first recorded in marsh 5 on 14 April 1965. On 6 July 1965, after 83 days, she was recaptured in marsh 2. The minimum direct distance between these two marshes is 124 m and includes a long open space that would seem to discourage dispersal. The female was captured again in marsh 1 on 26 July 1966, after 390 days. The distance traveled between the last two marshes was 33 m. Box turtles were most often observed on land on overcast days (see "Activity Temperature"). Webb et al. (1963:96) observed that T. coahuila moved overland ". . . in the rainy seasons . . . when intervening arid regions are wet."

About 20% of the T. coahuila recaptured in a span of more than a year and a half had made inter-marsh movements. Whether this reflects the true proportion of transients in the population of the study area, whether it indicates that T. coahuila make permanent shifts in their home ranges, or whether resident turtles react aggressively toward a newly-arrived immigrant in a marsh, are not known. T. coahuila in

Table 14. Duration of time spent in one marsh for 34 *Terrapene coahuila* recaptured at least once in a later sampling period. Ranges in parentheses.

Month in Which Turtle Captured For First Time	Number of New (unmarked) Turtles Captured in Month	Percentage Subsequently Recaptured	Mean Number of Months Elapsed Between First & Last Captures	Number of Turtles Recaptured in Same Marsh After One Year or Longer
December 1964	13	69%	11.1 (4 - 19)	4
April 1965	11	45%	9.6 (4 - 12)	5
July 1965	61	33%	7.8 (1 - 12)	5

the study area would seem to present a good opportunity to test the hypothesis of innate versus environmental dispersal of Howard (1960), and to determine what environmental cues are used in orientation during inter-marsh dispersal. Experiments of Gould (1957, 1959) indicate that *T. c. carolina*, when removed from their normal home range, employ sun orientation similar to that found in birds.

Aquatic turtles, *Chrysemys* and *Pseudemys*, tend to remain in certain home areas within lakes or ponds, but may shift their ranges to more favorable areas with changes in the immediate habitat (Cagle, 1944a; Sexton, 1959b). Turtles of these genera may make seasonal, overland movements or may be forced to move from a drying body of water. *Chrysemys picta* in Michigan emigrated annually in early spring from a small pond to several outlying bodies of water, and returned sporadically from summer to fall; 57% of the turtles did not return to the same area occupied the previous year (Sexton, 1959b). Sexton (1959b) classified the activities of *Chrysemys* which remained in the pond during summer as restricted, extralimital, or shifting. He estimated that 50 to 60% of the turtles had shifted the site of their activities to a new area from a previous one in which they had been sedentary. Average minimum distances between captures of 125 *Chrysemys* during summers of three different years were about 90 m; emigrating turtles moved an average of 156 m before leaving the pond and a minimum of 120 m overland to reach a nearby swamp (Sexton, 1959b). Legler (1960:634) believed that *T. o. ornata* occupied a single home range on his study area, but stated: "Females, because of their more extensive travels in the mating season, seem more likely than males to have multiple or changing ranges." Female *T. c. carolina* searching for nest sites moved from 249 to 775 m away from their home ranges, and one turtle regularly occupied two home ranges, traveling between them at infrequent intervals (Stickel, 1950).

POPULATIONS

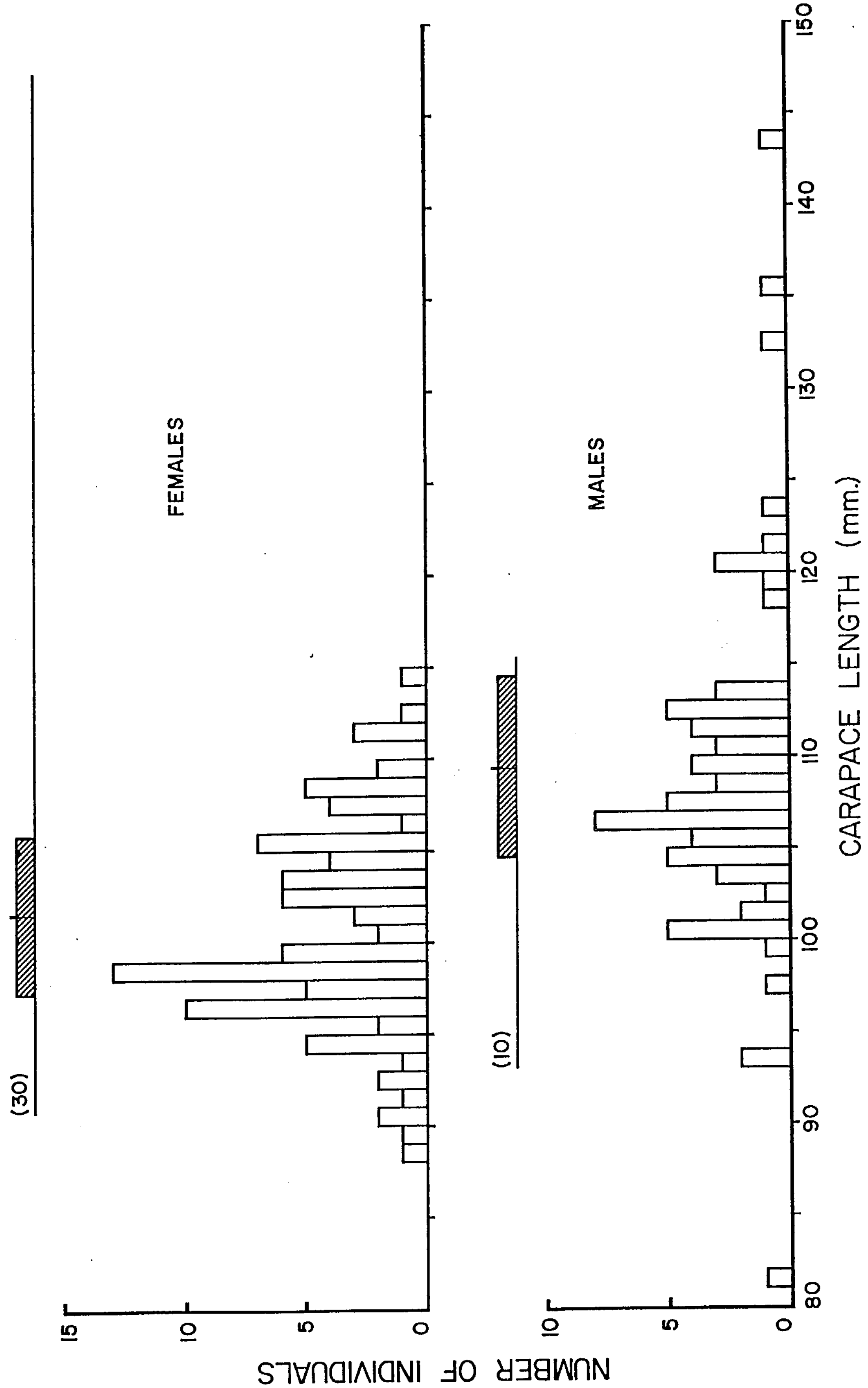
Composition

Through July 1966, 164 adult or subadult Coahuilan box turtles of known sex were captured in the field (sex of one subadult individual was not recorded). Three juveniles were found, comprising less than 2% of the sample taken from the population of the study area. The scarcity of young _T. coahuila_ probably results, in part, from their cryptic coloration and small size, making them much less conspicuous than adults. Also, they may be more secretive than larger individuals, hiding beneath mud or vegetation of marshes. A juvenile in marsh 6 on 15 July 1965 was discovered only after spotting a slight movement of its head withdrawing into mud beneath the water surface. Stickel (1950) and Legler (1960) noted many less juveniles than adults in populations of _T. c. carolina_ in Maryland and _T. o. ornata_ in Kansas. Stickel (1950) calculated that the juvenile segment of the _T. c. carolina_ population actually may have been much less numerous than the adult segment, although a greater difficulty in seeing and collecting young turtles may have been a factor. Legler (1960) attributed the rarity of juvenile _T. o. ornata_ more to their ability to escape notice than to a real difference in numbers.

For the most part, Coahuilan box turtles lack growth-rings, precluding aging by this method, so only the size distribution of adults and subadults can be shown (Fig. 24). Mean carapace length of 70 males (108.9 mm) is significantly larger than that of 94 females (100.9 mm) ($t = 6.79$, $P<0.01$). As indicated previously, there is also a significant difference between the mean size of males and females known to be sexually mature.

A comparison of the carapace length histogram of field-caught turtles with the bar diagram of size for sexually mature individuals of both sexes (Fig. 24) shows a close correspondence between the two; 73% of females and 77% of males fall above the value of the lower 95% confidence limit for size at sexual maturity (97.3 mm in females, 104.6 mm in males), and over 98% of both sexes in the field were larger than the smallest sexually mature individual in the preserved samples. Most turtles recorded in the field were, therefore, sexually mature or were approaching maturity. In the field samples, 34% more females than males fell in the size range 95 - 105 mm, and 32% more males than females were between 105 - 115 mm, the approximate 95% confidence ranges of sexual maturity for females and males, respectively. Modes of both samples are within the confidence ranges. A majority of turtles, especially females, are clumped at the lower end of the confidence range. Cagle (1954) observed a similar concentration of Chrysemys picta near the size of

Figure 24. Frequency distributions of body size in 164 *T. coahuila* (70 males, 94 females) from study area. Bar diagrams show size of sexually mature individuals examined in the laboratory. Horizontal and vertical lines represent range of observed variation and mean, respectively; blocks represent 95% confidence limits. Sample sizes in parentheses.


FEMALES
MALES
(30)
(10)
NUMBER OF INDIVIDUALS
15
10
5
0
10
5
0
80
90
100
110
120
130
140
150
CARAPACE LENGTH (mm.)

attainment of sexual maturity, attributing this to reduced growth at that time. Legler (1960) determined that growth in T. o. ornata stops about three years after reaching sexual maturity in both sexes, and there is a close agreement between his histogram of plastron lengths and percentages of sexually mature Ornate box turtles; the greatest number of individuals fall in the size groups having the largest proportion of mature individuals.

Of the 164 T. coahuila marked in the study area, 70 (43%) were males and 94 (57%) were females. The ratio of males to famales was, then, 1.00 to 1.34. There is an indication that the sex ratio varies seasonally, although females do not significantly outnumber males (as tested by chi square on the hypothesis of a 1:1 ratio) in any of the four monthly divisions of the season, or for the entire span of collections (Table 15). Reports of sex ratios in some turtle populations indicate a predominance of females (Hildebrand, 1932: Malaclemys terrapin; Risley, 1933: Sternothaerus odoratus; Cagle 1942: Chrysemys picta, Pseudemys scripta, and S. odoratus; Cagle, 1950: P. scripta; Tinkle, 1958b: S. depressus and S. carinatus; Sexton, 1959b: C. picta), but in others more males have been recorded (Cagle, 1952: M. terrapin; Ream and Ream, 1966: C. picta). In Terrapene, Legler (1960) found 37% males and 63% females of 164 adult T. o. ornata from Kansas (male/female ratio 1.00: 1.69). Nichols (1939a) reports 62% males and 38% females of

Table 15. Sex ratios of *Terrapene coahuila* marked in the study area from December 1964 through April 1966.

Month	Males		Females		Male:Female Ratio	X^2	P
	n	%	n	%			
December & January	14	50.0	14	50.0	1.00:1.00	--	--
April	12	44.4	15	55.6	1.00:1.25	0.15	>0.70
July	28	43.7	36	56.3	1.00:1.29	0.77	>0.30
August	16	35.6	29	64.4	1.00:1.81	3.20	>0.05
Combined	70	42.7	94	57.3	1.00:1.34	3.22	>0.05

387 _T. c. carolina_ from New York (male/female ratio 1.60: 1.00), but Stickel (1950) recorded 48% males and 52% females in 245 adult _T. c. carolina_ from Maryland (male/female ratio 1.00:1.09). Discrepancies are apparent in reports of _Chrysemys picta_, _Malaclemys terrapin_, and _Terrapene c. carolina_. These differences are due largely to the following factors: (i) seasonal differences in activity, as in _Malaclemys_, where Cagle (1952:74) points out that "The large number of males /4.4 males per female/ in the present group may reflect the apparent tendency of females to move toward shore during the egg-laying season"; (ii) a sexual difference in size when secondary sex characters appear or when the turtles become sexually mature, and the interpretation of this difference; and (iii) different sampling techniques employed. Ream and Ream (1966) have investigated the last factor. They found significant differences between juvenile: female:male ratios of _C. picta_ in four of five sampling methods tested.

The second factor listed above appears to have caused the great disagreement in sex ratios reported in the literature, even between populations of the same species not widely separated geographically. Cagle (1942) first pointed out that for species of such genera as _Pseudemys_, _Chrysemys_, and _Graptemys_, in which females reach maturity at a much larger size than males, the sex ratio can be altered (shifted upward in favor of males) by eliminating immature females that overlap mature males in size. Thus, Sexton (1959b) reported an "actual" male/female ratio of 1.00:1.49 for 604 Chrysemys picta of known sex in Michigan, but when he considered only sexually mature individuals, the ratio became 1.32:1.00, closely approximating the 1.30:1.00 ratio for a Minnesota population of the same species reported by Ream and Ream (1966), who had distinguished juveniles from adult males and females throughout their study. The widely-divergent results of Nichols (1939a) from those of Stickel (1950) on the sex ratio of T. c. carolina seem to result partly from this error (Stickel distinguished between juveniles, subadults of intermediate size, and adults with observable secondary sex characters), and partly because his sex determinations were based solely on four arbitrary categories of relative plastral indentation (without first sexing the turtles when they were captured in the field by using a combination of characters).

As indicated above, most T. coahuila in my samples were sexually mature, so the sex ratios given (not considering juveniles) most likely show an actual difference in population structure due to sex alone, but, to some degree, may also reflect a departure from any real difference, such as could be caused by a possible seasonal shift in activity. If, for example, females are inclined to travel more often or farther in search of nesting sites during the reproductive period, the probability of their capture would be increased.

No direct data, other than the sex ratios themselves, are presently available to support such an hypothesis.

Density

The study area can be divided into two sections: a primary section (main study area) of 11 marshes sampled regularly, and a secondary section of marshes surrounding the main area. The last marshes were not included in daily field sampling. Although the choice to limit the study area to a given series of marshes was somewhat arbitrary, considerable distances of unfavorable habitat separate marshes in the main area from outlying ones. In some instances, however, the distance from any marsh in the study area to an outlying marsh was less than the extreme distance between two marshes at opposite sides of the study area proper (about 600 m). Population estimates are likely to be affected by turtles moving between main and surrounding marshes, but the extent of immigration and emigration was difficult to estimate due to the limited time of this study. There are reasons (considered below) suggesting that these factors caused negligible error in the census.

Between 30 December 1964 and 15 October 1966, I marked 169 individual T. coahuila (three juveniles, 166 subadults or adults) in the entire study area. There were 271 captures of these individuals, of which 163 (60%) were recaptures. In outlying areas, three marshes located about

0.8 km east of the 11 principal marshes were not sampled for the first time until 14 August 1965. Twenty-five individuals were captured in these marshes, and 26 turtles were marked in other marshes, posas, drainage channels, or on land (termed miscellaneous areas). Most, but not all, of the turtles marked in the last group of habitats were outside the main study area. Since 25% of these individuals were captured within the main study area, but not in a sampled marsh, a small source of error (tending to underestimate the population) is possible. None of these turtles was subsequently recaptured. Three individuals initially were marked considerable distances away from the main area marsh in which they were later recaptured. Of the 169 individuals, five were first captured in marsh 4, located near the main study area. This marsh was not sampled regularly, and is considered as a "miscellaneous area." One individual from this marsh was recaptured later in a main marsh, and together with the three turtles mentioned above, is counted as a "new" individual in the main study area. Two individuals that had been marked in December 1964 and in April 1965 were found dead on 2 July 1965. These turtles constitute the only mortality of marked animals, and they were subtracted from the figures before applying them to census formulas, even though mortality would not affect the results as long as it is the same for both marked and unmarked animals. Thus, four turtles were added to 114 turtles captured in the main area, giving 118 first-capture individuals. This figure was reduced by mortality (two) for a total of 116 used in all computations on census samples taken after July 1965 (Table 16).

The four turtles that entered the area and were added to the samples would raise the population size estimated by the single census or Lincoln Index, but the error caused by their addition is slight, considering the generally-adequate sample sizes obtained. Also, it is assumed that the probability of emigration is equal to immigration, balancing any influx of marked or unmarked turtles. Although I did not sample surrounding districts as thoroughly as the main study area, a roughly equal proportion of marked vs. unmarked turtles could enter as well as leave the study area, particularly in the early phases of field work when the percentage of marked animals in the main study area was low.

An important assumption of mark-recapture sampling is that the balance between marked and unmarked animals remains undisturbed between sampling periods (Hayne, 1949b; Stickel, 1950; Ricker, 1958). As noted above, a few transient _T. coahuila_ can be expected in collections from the study area. Stickel (1950:374) observed that disturbance of the ratio of marked to unmarked animals caused by an influx of transients ". . . is not likely to be large enough to be significant except under unusual circumstances, when there is a very large transient population."

Table 16. Data used to calculate size of <u>Terrapene coahuila</u> population in main study area. Asterisks locate mortality of two marked individuals subtracted from indicated figures prior to census calculations.

Marsh No.	Number of Individuals Captured for First Time in Marsh	Number of Subsequent Recaptures in Same or Different Marsh	Total Number of Captures
1	5	8	13
2	5	5	10
2-A	6	4	10
3	14*	15	29
5	11*	8	19
6	10	12	22
8	5	3	8
8-A	4	2	6
9	4	1	5
10	5	4	9
11	49	23	72
Total (11 marshes)	118*	85	203

Table 16, continued.

Period of Field Work (Number of days when one or more turtles captured)	Number of Individuals Captured for First Time in Period	Number of Recaptures of Individuals Marked in Same or Previous Period	Total Number of Captures
December 1964 (2)	13	0	13
April 1965 (1)	11	5	16
July 1965 (25)	61*	19	80
August 1965 (16)	15	15	30
December 1965 & January 1966 (5)	4	12	16
April 1966 (4)	10	19	29
July, September, & October 1966 (4)	4	15	19
Total (57 days)	118*	85	203

The following observations provide evidence that recruitment of the population by immigration, or loss by emigration, are relatively unimportant factors in affecting the precision of the estimated number of T. coahuila inhabiting the study area: (i) marshes are distinct communities with sharply-defined borders, and box turtles are largely confined to them; (ii) although some overland movements do occur, salt grass communities in surrounding dry, often bare, zones are effective barriers to dispersal of T. coahuila—the main study area is fairly well set off from other marshes by these unfavorable regions; (iii) recaptures of Coahuilan box turtles show that they have a tendency to remain in one marsh for long periods (more than a year in 41% of 34 recaptured turtles, and more than a year and a half for two individuals); (iv) population size from December 1964 through April 1966 in the main study area was relatively stable (Table 17), and the proportion of individuals recaptured increased from 8% to over 75% as the study progressed. This suggests that replacement of the population by unmarked animals was minimal (see Hayne, 1949b). The problem confronting Stickel (1950) of accounting for animals whose home range overlaps the edge of a study area in continuous favorable habitat was not present in my study, since the edge of a marsh presented a real barrier to T. coahuila.

The 114 T. coahuila that were marked in the main study area were captured a total of 203 times. Thirty-one

(27%) were recaptured once, nine (8%) twice, nine (8%) three times, two (2%) four times, and one individual (1%) was recaptured five times, the maximum number of recaptures obtained. Slightly less than half (46%) of the individuals in the main study area were recaptured at least once, compared to only 36% of the 169 individuals that were recaptured over the entire area. The higher proportion of recaptures in the main area, resulting from longer and more regular sampling, and the partial ecological isolation of the main area from surrounding regions, lend support to the separation of its turtle captures, and to their treatment as a unit distinct from other records in the census computations.

A second major assumption concerning the sampling is that all animals in the population, both marked and unmarked, have equal chances of being collected. Although the marks themselves did not affect a turtle's probability of being captured, there is some evidence that an adverse effect on the behavior of marked T. coahuila occurred in the field, causing frequencies of capture of the various recapture classes to deviate slightly from frequencies expected on the basis of random occurrence. Frequencies of occurrence of recapture classes should follow a Poisson distribution if individuals recaptured once, twice, three times, etc., are distributed throughout the population at random and all have a random but equal chance to be captured. Departures from the Poisson distribution would indicate that any recapture class has a chance of capture greater than or less than random expectation.

The Poisson distribution was calculated for the 114 individuals captured 203 times in the study area. A highly significant departure from the Poisson series was indicated (pooled $X^2 = 16.6$, $P < 0.0001$) for four recapture classes in the distribution (0, to 3 or more recaptures). Calculated differences between the observed and expected number of capture records for each recapture class, with chi-square and probability values in parentheses, are as follows: 0 recaptures, 9.8 greater than expected ($X^2 = 1.84$, $P > 0.10$); 1 recapture, 9.8 less than expected ($X^2 = 2.35$, $P > 0.10$); 2 recaptures, 6.9 less than expected ($X^2 = 3.02$, $P > 0.05$); and 3 or more recaptures, 6.9 greater than expected ($X^2 = 9.43$, $P = 0.002$). Individuals were generally less susceptible to second and third captures, but were significantly prone to be captured four or more times. In most marshes, box turtle activity seemed to decline markedly after several successive days of capturing turtles. This was followed by a period of the next several days, or even weeks in some marshes, without captures. Marked box turtles seemed to move into seclusion. Because of my activity, they could also have become more wary during July and August 1965 when the study area was visited daily, lowering second or third captures. In subsequent sampling periods, after monthly intervals during which there was no intruder present, a restoration of normal activity could have occurred and recaptures would be shifted upwards. Tinkle (1958a) observed that marked Pseudemys and Graptemys in rivers were more wary than unmarked turtles, and Sexton (1959b) found it difficult to recapture marked Chrysemys picta from a boat in open water, although unmarked individuals could be approached and netted with relative ease. In the T. coahuila data, however, the possibility of a deviation from expected results by errors of random sampling should not be dismissed.

Records of capture of T. coahuila in the main study area that were used in the census computations are in Table 16. One juvenile, the smallest of three recorded, was excluded from these figures. Two of the juveniles were included because they were near subadult size (72.0 and 73.4 mm carapace length). Accordingly, estimates of numbers and density of the population apply to more than 98% adults.

Three census techniques were used on the mark-recapture data to estimate the size of the population. The first, a single census method (Petersen or Lincoln Index), has been widely used in population ecology studies. A preliminary sample of animals is marked and released into the population, and a follow-up sample is taken later and examined for marked animals. The ratio used to calculate population size (P) when the first sample was taken may be expressed as follows:

$$\frac{P}{\text{number of animals marked in first sample}} = \frac{\text{total number of animals caught in second sample}}{\text{number of recaptures (marked animals) in second sample}}$$

H. S. Fitch (1963, 1965), working with snakes, divided the season's records into monthly intervals and then successively lengthened the preliminary sampling periods, obtaining population estimates at different points in time through a collecting season. I sampled the *T. coahuila* population 10 times between December 1964 and October 1966. Each sampling period was separated by intervals of two to four months, but records were treated as seven units to obtain workable sample sizes (Table 16). Successively increasing the first samples gave six population estimates by the single census ratio. For example, of the 83 turtles marked from December 1964 through July 1965, 37 were recaptured along with 33 new turtles in the period August 1965 through October 1966, and the formula may be stated: $\frac{P}{83} = \frac{70}{37}$, or P = 157. The population estimated by single census ratios ranged from 146 to 171 individuals, or a density of 53.7 to 62.9 turtles per acre.

A modification of the Lincoln Index census was presented by Hayne (1949b). With continued sampling of the population, recapture ratios steadily rise as the pool of marked individuals grows. The total population can be estimated by projecting the trend of the increasing proportion of marked animals (see Hayne, 1949b, for details of procedure).

Using the same census samples (Table 17), percentages of recaptures to total captures in each of the six follow-up periods were: April 1965 - October 1966, 8.0%; July 1965 - October 1966, 14.0%; August 1965 - October 1966, 52.9%; December 1965 - October 1966, 64.0%; April 1966 - October 1966, 65.9%; and July 1966 - October 1966, 76.5%. Population size calculated by the Hayne method was 149 - a density of 54.8 turtles per acre.

Another technique is the multiple census, or Schnabel method, in which animals are marked and released into the population, and samples are taken and examined for recaptures, continuously over a considerable period. Each day's catch is treated as a separate census. The method attempts to reduce errors of random sampling encountered in single censuses by combining the data from successive daily sampling of the population. I used Schnabel's short formula (in Ricker, 1958), which is:

$$P = \frac{\sum(C_t \; M_t)}{\sum R_t}$$, where M_t = total number or marked animals at large when day t, the next sampling interval, begins (a cumulative number, less known mortality or removals); C_t = total number of individuals captured on day t; and R_t = number of recaptures in the sample, C_t. There was a total of 57 days on which box turtles were caught in the main study area, so 57 samples were available for use in the

formula. Prior to calculations, corrections were made for two marked turtles found dead in the study area, and for two individuals removed from marsh 11 for food habits study. The population indicated by the multiple census was 164, or 60.3 turtles per acre. As outlined in Ricker (1958), 95% confidence limits were calculated for P. The probability is 0.95 that 135 and 208 include the true population size, and that 49.6 and 76.5 turtles per acre include the actual population density in the study area. Results from the three census methods are summarized and compared in Table 17.

Marshes and other favorable habitats within the restricted geographic range of T. coahuila constitute its ecological range. Considering all 11 marshes in the main study area as a unit, the total ecological range is 2.72 acres (1.10 hectares). Population densities reported here for T. coahuila are based on this total area, not on each separate marsh. The main reason for this is that 21% of the turtles recaptured in a sampling period after they were first marked had changed marshes. Inter-marsh dispersal is a factor that could lead to extreme variations in density for a single marsh. Also, sample sizes from individual marshes were too small for precise census estimates. The population density calculated for T. coahuila (roughly 60 turtles per acre) is, therefore, an average density for all marshes in the main study area. It does not take into account

Table 17. Number and density of *Terrapene coahuila* in main study area of 11 marshes (total area 2.72 acres, or 1.10 hectares) from December 1964 to October 1966 calculated by three different methods (see text for details). Ninety-five per cent confidence limits are given in parentheses for Schnabel method. To obtain density of turtles per hectare, mulitply turtles per are x 100.

Method	Sampling Periods		Estimated Population Size	Population Density	
	Preliminary	Follow-up		Turtles/Acre	Turtles/Are (100 m^2)
Single Census: Petersen Type, or Lincoln Index.	Dec. 1964	April 1965 Oct. 1966	162	59.6	1.47
	Dec. 1964- April 1965	July 1965 Oct. 1966	171	62.9	1.55
	Dec. 1964- July 1965	Aug. 1965 Oct. 1966	157	57.7	1.43
Fitch's successive lengthening of sample periods.	Dec. 1964- Aug. 1965	Dec. 1965 Oct. 1966	153	56.3	1.39
	Dec. 1964- Jan. 1966	April 1966 Oct. 1966	155	57.0	1.41
	Dec. 1964- April 1966	July 1966 Oct. 1966	146	53.7	1.33
Hayne Method; increasing proportion of recaptures	Six census samples used above		149	54.8	1.35
Multiple Census: Schnabel Type.	Daily (57 capture-days)		164 (135 - 208)	60.3 (49.6 - 76.5)	1.49 (1.23 - 1.89)

spatial relationships of turtles within the marshes. Captures were clumped in open areas, probably because turtles were more easily seen there than in areas of dense vegetation.

Few precise data on population densities in natural populations of turtles are available in the literature. Often, population studies have compared relative abundance of different species from various aquatic habitats in which it is difficult to obtain a reliable estimate of numbers (Cagle, 1942; Cagle and Chaney, 1950; Tinkle, 1958a, 1959b). Cagle (1942) estimated numbers of *Chrysemys picta* and *Pseudemys scripta* elegans in two small stock ponds in Illinois. Densities calculated from his data are as follows: *C. picta*, 141.8 and 555.6 turtles per acre (3.6 and 13.9 turtles per are); *P. s. elegans*, 72.2 and 206.3 turtles per acre (1.8 and 5.2 turtles per are). Cagle reported that a 145-acre reservoir in Illinois contained 1,580 *P. s. elegans*, or approximately 11 turtles per acre. His estimate of the population was in error, however, since several hundred animals had been previously removed from the reservoir. Pearse (1923) estimated a density of 5.02 *Chrysemys picta* per acre in a shallow bay of 547 acres in Lake Mendota, Wisconsin. He estimated densities of about 15 to 20 turtles per acre in vegetated areas. From the size of the *C. picta* population estimated by Ream and Ream (1966) working in the same bay, calculated density is 1.63 turtles per acre (using the area of 547 acres given by Pearse). Sexton (1959b) reported densities varying between 40 and 166 *C. picta* per acre (depending on surface levels) in five Michigan ponds.

Several careful population density estimates have been made for the genus *Terrapene*. Stickel (1950) calculated a density of 4.5 *T. c. carolina* per acre in favorable habitat in Maryland, and gave between 4 and 5 adult turtles per acre as a reliable approximation of the true density on her 30-acre study area. *T. c. carolina* occurred at a density of 3.6 turtles per acre in Indiana (Williams, 1961). Legler (1960) estimated the population density of *T. o. ornata* on 220 acres of grassland in Kansas to be 1.3 turtles per acre. In the most favorable pasture habitats, densities were higher: 2.6 to 6.3 turtles per acre (Legler, 1960).

The aquatic *T. coahuila* occurs at considerably higher population densities than its terrestrial congeners, *T. c. carolina* and *T. o. ornata*. Sixty turtles per acre probably represents a typical population density in most small marshes in the basin. Population densities reported for a few species of aquatic emydines are extremely variable, but variation undoubtedly resulted as much, if not more, from sampling errors as from actual differences between populations. *T. coahuila* occurs in densities roughly comparable to some of these aquatic species, such as *Chrysemys picta*.

Mortality and Replacement

Proper analysis of the dynamics of any population requires data on age-specific survivorship and fecundity (Deevey, 1947; Hutchinson and Deevey, 1949; Andrewartha and Birch, 1954; Slobodkin, 1961). Birth rates and death rates depend strongly on the age distribution of the animals, and even density may mean little without some knowledge of the population's age structure. Unfortunately, Coahuilan box turtles were not aged and no natural size groups that might indicate age were apparent.

I have seen one estimate in the literature (that of Legler, 1960, below) of mortality rates in any phase of the life cycle of turtle populations. Probable reasons for this lack of information are the comparatively low year-to-year mortality of adult turtles and their relatively long life span, making it difficult to follow a natural population or cohort of individuals of known age for the many years that would be necessary to measure age-specific mortality. Mortality has been estimated, however, in certain natural populations of other reptiles (Blair, 1960; H. S. Fitch, 1958, 1960, 1963, 1965). Mortality seemed high among adult _T. c. triunguis_ during hibernation in Oklahoma (Carpenter, 1957). In three years on 60 acres, Carpenter (1957) recorded 473 _T. c. triunguis_ and 91 shells of dead individuals. I found shells or old skeletal remains of 18 _T. coahuila_ in the study area (mostly on land), but this gives little indication of the actual mortality affecting the population. Infertility and prenatal mortality may take the greatest toll in many turtle populations. Legler (1960) incubated eggs of T. o. ornata (about 14 clutches) in the laboratory of which only 60% hatched successfully.

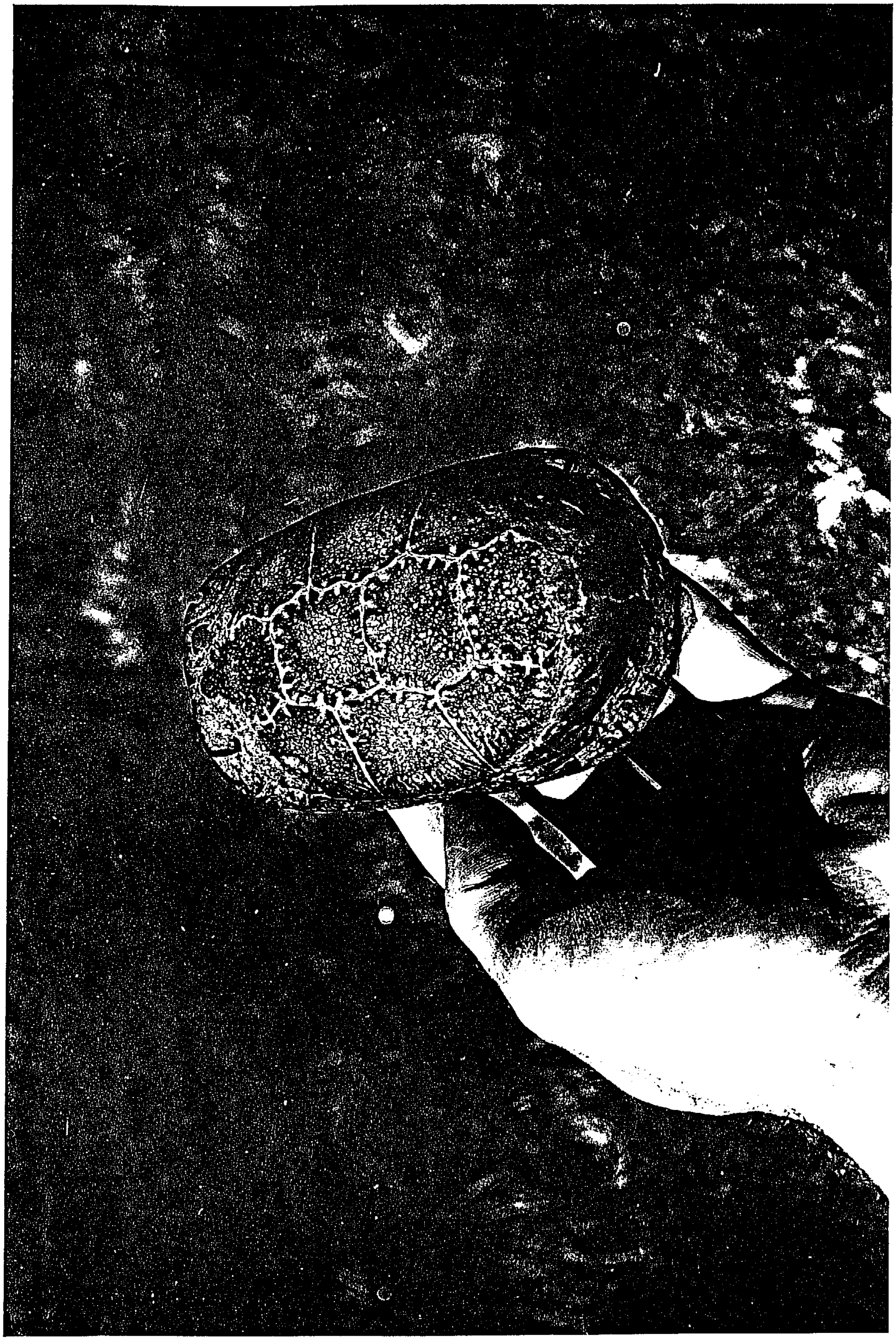
The population of T. coahuila studied is composed of approximately 57% adult females, or 90 capable of reproduction, given an adult population of 160 individuals in the study area. The annual egg production of these females may be approximately 400 eggs per season if all 90 deposit at least a single clutch averaging 2.7 eggs (240 eggs produced), if 47 (53%) deposit a second clutch averaging 2.4 eggs (110 eggs produced), and if 31 (35%) deposit a third clutch averaging 1.7 eggs (50 eggs produced). If individuals lost each season through mortality are to be replaced and a stable population maintained, but if adult mortality is low, a total annual complement of 400 eggs could suffer rather high losses from the time of laying to the time when sexual maturity is attained and females are capable of reproducing according to the above schedule. An important assumption is that after being replaced by survivors from the previous egg complement, fecundity of the female segment of the population is constant during the interval necessary to produce the next total set of 400 eggs. Since fecundity in any animal population varies with the age of the female, it is unlikely that this assumption is entirely valid.

Coahuilan box turtles are the largest and most noticeable element of the reptilian fauna living in many of the small, spring-fed marsh communities in the Cuatro Ciénegas basin. Yet their precise role in the ecology of these marshes will remain largely unclarified until a satisfactory aging technique can be developed and ecological life tables constructed so that population productivity as it relates to other organisms may be more precisely defined. Other marsh-inhabiting organisms in the basin, both plant and animal, vertebrate and invertebrate, need to be investigated to further clarify the various ecological interrelationships occurring between their populations and the *Terrapene coahuila* population, and between all of these and the components of their environment.

PARASITES AND INJURIES

Although frequency of occurrence was not recorded, some _T. coahuila_ possessed compact deposits of algal marl on the carapace. These layers were most common on the anterior or posterior edges, or both (Fig. 25). Two individuals collected on 20 December 1965 from a seep near the Mojarral lagunas had algal encrustation on the five posterior marginal scutes of each side, the posterior portion of the third costals, and all of the fourth costals on both sides of the shell; one possessed coatings on the first two marginals anteriorly. Color of these deposits on _T. coahuila_ range from a pinkish hue to green. Samples were scraped from carapaces of five individuals from marshes in or near the study area; three in December 1965 and two in January 1966. Six genera of blue-green algae (Cyanophyta) were identified from these samples and are as follows (followed by number of turtles on which found, in parentheses): _Anacystis_ (1), _Gloeothece_ (5), _Lyngbya_ (3), _Oscillatoria_ (2), _Pleurocapsa_ (5), and _Spirulina_ (1). Diatoms occurred on two of the turtles along with five of the blue-green genera. No green algae (Chlorophyta) were in any of the samples from turtle carapaces, but a sample of algae collected from marsh 2 in January 1966 contained the green algae _Spirogyra_ and _Mougeotia_. A blue-green alga (_Gloeothece_) and diatoms (_Synedra_

Figure 25. Male *T. coahuila* (carapace length 105 mm) from marsh N-3, 27 January 1966. Blue-green algae, *Gloeothece* sp. and *Pleurocapsa* sp., were in a sample obtained from prominent algal deposits on anterior and posterior carapace of this individual.



and others) were also present in the marsh sample. A. T. Hotchkiss (personal communication) believed that the blue-green algae were on _T. coahuila_ shells largely by chance and that they might well have occurred on any other solid substratum. Except for one unidentified blue-green alga, none of the forms was an "attached alga" to the extent of having a holdfast. Many species of aquatic turtles support floras of epizoic green algae, composed mainly of the genus _Basicladia_ (Edgren et al., 1953; Neill and Allen, 1954; Moski, 1955, 1957; Proctor, 1958; Walker et al., 1953). _Basicladia_, a genus restricted mostly to turtles, was not on any of the _T. coahuila_ from which samples were taken. However, a filamentous algal growth that was not identified (but which may have been _Basicladia_) was on the carapace of an individual in the preserved series from near the study area. One individual, captured in July 1965 in the study area, had six small, round "pits" about 1 mm deep and a larger pit about 7 mm in diameter and 2 mm deep, on the second right costal scute. Pitting and eventual erosion of the shell in aquatic turtles may be caused by an invasion of certain algae or fungi under the epidermal laminae (Hunt, 1957, 1958). Potter (1886, 1887) described the penetration of wedge-shaped masses of the green alga, _Dermatophyton radicans_, into the carapace of _Clemmys caspica_ (= _Mauremys caspica_, _sensu_ McDowell, 1964) of Europe as follows: "The cells next to the tortoise shell are closely adpressed to it, and individually have the power of penetrating into any crack of the tortoise shell which may present itself to them. When an algal cell meets with a crack, it strives to penetrate into it, in doing which it opens the crack more and more and so penetrates further in . . . [Potter, 1887:252]." Jackson (1964) noted carapace erosion in *Sternothaerus m. minor* from Florida, and Carpenter (1956) recorded carapace pits in *T. c. triunguis* in Oklahoma. Neither author could give a probable cause for the shell erosion in these two species, but Carpenter (1956) speculated that parasitic fungi, among other factors, might be involved.

Seven of 169 (4%) Coahuilan box turtles in the field harbored 1 to 4 small leeches (Hirudinea) attached to the skin at the base of the tail or to the posterior ventral margin of the carapace. Leeches did not exceed a length of approximately 1 cm, and did not appear to cause discomfort to turtles; they were easily detached.

Internally, 46% of 48 dissected *T. coahuila* contained from 1 to 5 small nematode worms in the stomach, some of which were imbedded in the lining. A total of 68 nematodes was in 22 stomachs; they averaged 2.4% of the volume of material in stomachs possessing them. Nematodes in the latter turtle were matted together in two compact aggregations. Webb (1961: 213) recorded "Numerous nematodes, four small flukes and a tapeworm . . ." from intestines of *Graptemys pseudogeographica* in Oklahoma.

Injuries were noted in 24 of 218 (11%) T. coahuila examined in the field and in the laboratory. Of these, seven (3%) were burn scars, six (3%) were limb amputations, and six (3%) were scars on the shell attributable to predators. Burning of grasses is practiced in the basin of Cuatro Ciénegas. Burn scars on the carapace usually covered between one-fourth and one-half of the surface area and consisted of rough-textured, regenerated epidermis, recently-exposed underlying bone, or raised patches of dead bone sloughing from an old wound. Legler (1960:642) described the old bone during shell regeneration in burned T. o. ornata, stating: "Areas of exposed bone become white and shiny, nearly enamellike in appearance, as a result of wear on the shell." I observed this in five of seven burned specimens of T. coahuila. The worst burn injury recorded was in a subadult male (ASU 05854) collected in July 1965 near the study area. All epidermal scutes of the carapace had been burned away, and the exposed bone was smooth and polished, lacking noticeable sutures, as if it had been melted. The epidermis of most of the marginal scutes was loose and peeling away. The turtle appeared healthy and its stomach contained food.

Amputations and some carapacial scars probably result from attacks by predators. One of the hind limbs was missing in four of five adults with amputations, and the other lacked its right foreleg. The post-hatchling (ASU 08000) lacked most of its right hind foot and the right posterior portion of its carapace was gouged away. Four individuals had long, shallow gashes through the epidermis of the shell that could only have been inflicted by some large predator. A male in marsh N-2 on 4 April 1966 had a long (4 cm) gash on the second left costal scute, and several small pock-like scars (presumably tooth marks) on the carapace and plastron. In addition, the right hind leg was missing. This individual had evidently been mauled by a predator. One animal that could inflict wounds of this nature,and possibly succeed in preying on some turtles, is the coyote, Canis latrans. A coyote was seen crossing the study area one early morning during the summer of 1965, but no obvious sign of their presence was otherwise noted. Minckley (1966) described a coyote catching a large Pseudemys scripta taylori in a shallow lake in the basin about 22 km southwest of Cuatro Ciénegas, and found a live T. coahuila that had been attacked and chewed by a coyote at the same locality.

Coahuilan box turtles are extremely alert when foraging and seem to rely mainly on escape for survival (see "Foraging Behavior"). When T. coahuila were handled in the field during this study, they all pulled the lobes of the plastron tightly against the carapace and remained closed until left undisturbed for several minutes. There was no variation in this reaction. Nichols (1939b) and Legler (1960) have noted that some T. c. carolina and T. o. ornata struggle to escape while handled, whereas others close their shells and remain passive.

As previously mentioned, T. coahuila occasionally enter posas (Fig. 8) in the study area. Tracks were frequently seen across the mud bottom of all three posas in the study area, but the turtles themselves were rarely encountered. Several were seen, however, and an attempt was made to catch them, but they easily eluded capture in most instances by swimming rapidly along the bottom, under 20 to 50 cm of water, and disappearing beneath the undercut banks. T. coahuila reminds one of Sternothaerus or Kinosternon in their rapid and elusive swimming ability. Milstead (1967:178) called T. coahuila an "awkward swimmer", but I cannot subscribe to this. From the individuals that I have observed in posas containing relatively deep water, T. coahuila is remarkably agile.

As are other aquatic animals living in a region where water for human development is at a premium, the Coahuilan Box Turtle could become threatened by extinction. Canals carrying water for irrigation have already destroyed one extensive aquatic habitat (Posas de la Becerra) in the basin in December 1964 (see Cole and Minckley, 1966). A carefully planned program of development for the region to gain effective use of the water supply will be essential to prevent a general lowering of the water table and associated surface waters so vital to many of the unique, and often rare, plants and animals inhabiting the basin. Populations of T. coahuila in the marshes are relatively dense and the species may be able to withstand some diminishing of its numbers by collectors, so destruction of its habitat presently represents the main threat. But because of zealous interest by herpetologists in rare animals whose habits and adaptations are so unusual, the existence of _T. coahuila_ could also be placed in jeopardy through over-collecting by curiosity seekers in combination with the first factor. Where at all possible, the critique of Duellman (1966) should be heeded and future collections of _T. coahuila_ should be made only by investigators with a specific problem concerning the species and with proper governmental authorization to collect it.

SUMMARY

1. A relict population of the only aquatic box turtle, *Terrapene coahuila*, was studied during nine periods varying from 1 to 60 days between December 1964 and October 1966 in its natural habitat in northern Mexico.

2. *T. coahuila* lives in distinct aquatic habitats within an interior basin of the Chihuahuan Desert located near Cuatro Ciénegas, Coahuila, on the northern Mexican Plateau. The geographic range of the species consists of disjunct populations in an area that does not exceed 800 km^2.

3. *T. coahuila* was studied most intensively 10 km southwest of Cuatro Ciénegas near the northeast tip of Sierra de San Marcos. In this area, box turtles inhabit small, north-south trending, spring-fed seeps, or marshes, characterized by mud bottoms, shallow water, and dense aquatic vegetation. Principal marsh plants are *Eleocharis rostellata*, *Scirpus olneyi*, and *Baccharis glutinosa*. Marshes are distinct from surrounding desert which is vegetated by sparse grasses and shrubs (mainly *Distichlis stricta*, *Allenrolfea occidentalis*, and *Prosopis juliflora*).

4. Coloration of *T. coahuila* is brown, blending well with the mud bottom of marshes. About 70% of adult turtles

possess a vermiculated pattern of small, yellow markings on the carapace. Because nearly all adults lack growth-rings, growth and age could not be determined by this method. Plastron length at hatching is estimated to be 26 to 29 mm. Calculated plastral length increases of 20% and 49% were made by two juveniles in their first full season of growth.

5. Seventy adult males from the study area averaged 108.9 mm in carapace length, and 94 adult females averaged 100.9 mm. Individuals from the study area are considerably smaller than all United States subspecies of _Terrapene_, and average smaller than _T. coahuila_ from other localities in the basin.

6. Six bi-variate relations between seven carapace and plastron measures were developed for 70 males and 94 females. Strongest sexual dimorphism was indicated in the carapace height/carapace length relationship, with males having a relatively lower carapace (average height/length ratio about 43%) than females (average height/length ratio about 46%). Other sexual differences are the concave posterior plastral lobe of males (flat in females), the longer and thicker tail of males, and the brownish eye of males (yellowish in females).

7. Eleven (5%) of 218 _T. coahuila_ had extra epidermal

scutes or had less than the normal number, and five had incomplete or abnormal interlaminal sutures.

8. Mating in _T. coahuila_ occurs from September to June and is most concentrated in March and April. Copulating pairs of box turtles were found in the study area in December 1964 and in April 1966. Mating occurs in shallow water.

9. Sperm were most abundant in epididymal smears of males in April, and were numerous in smears from individuals with enlarged testes in late August. Testes were small in specimens from April and July, but had increased greatly in size by late August. Data on testes size and relative abundance of sperm tentatively suggest a spermatogenic cycle similar to northern _Terrapene_. With a long period of sexual activity in the warm southern environment, spermatogenesis may be extended long into the winter.

10. Follicular enlargement occurs between late August, when ovarian weights are low, and early April when ovaries are heavy and when nearly all mature females have one or more enlarged follicles in the ovaries. Ovulation begins in early April. There is an alternation of ovarian activity, with one ovary usually more active than its partner in a given reproductive period.

11. Sixteen female _T. coahuila_ representing 23 actual or potential clutches indicate that complements of 2 or 3

eggs are produced most frequently, with an over-all mean clutch size of 2.3 (range 1 to 4). About half of the population can produce second clutches, and about one-third of the population appears capable of laying three sets of eggs in a season. Initial oviposition is probably concentrated in May. Clutch sizes decrease from a mean of 2.7 eggs in the first clutch to 2.4 in the second and 1.7 in the third. The maximum annual reproductive capacity may amount to 11 eggs, but the mean reproductive potential, realized by about one-third of the population, is 6.8 eggs/female per season. Egg laying begins in late April and early May and continues to late September. Hatching probably occurs as late as November or December. No nests of T. coahuila have been discovered. Nine oviducal eggs in three gravid females averaged 33 x 17 mm, and 6 g in weight.

12. Box turtles foraging in marshes move in shallow water, with the carapace above the surface and head extended underwater; the forelegs are used to expose places in vegetation for feeding. The animals pause frequently to survey their surroundings. In feeding habits, T. coahuila is opportunistic and omnivorous. Staple items in the diet are stems and seeds of the spike-rush, Eleocharis rostellata; stratiomyid Diptera larvae; curculionid beetles; nymphs of libellulid dragonflies and agrionid damselflies; mayfly nymphs; and naucorid bugs. Spiders and crustaceans appear in lesser amounts. Live fishes are rarely eaten, mainly because box

turtles are unable to catch them.

13. Body temperatures of T. coahuila active in marshes closely approximate temperatures of the surrounding water. During July and August 1965, cloacal temperatures of most individuals were approximately 1 C below the surrounding water in the morning, but during the afternoon most were slightly warmer than the medium. There is wide seasonal variation in the mean body temperature of active turtles; mean cloacal temperatures in December and January are about 21.0 C, in April about 26.0 C, and in July and August about 28.0 C. A voluntary minimum temperature of 14.8 C and a voluntary maximum of 33.5 C were the extreme body temperatures recorded at all seasons within marshes. Cloacal and water temperatures fluctuated significantly with time of day in July and August 1965; between 6:00 and 7:00 AM, body temperatures averaged about 25.0 C, and between 4:00 and 5:00 PM body temperatures averaged about 31.0 C. Coahuilan box turtles are occasionally active away from marshes in summer under overcast skies. Basking was recorded in December 1965 when three turtles on land had cloacal temperatures raised from 6.5 to 14.0 C above air temperatures.

14. In summer, Coahuilan box turtles are active mainly in early morning and late afternoon; activity is also nocturnal. The maximum temperature voluntarily tolerated by T. coahuila

is about 35.0 C, and water temperatures in marshes during summer at mid-day are often above tolerable levels. Marsh bottoms provide a cool refuge into which a turtle can easily retreat by burrowing to avoid potentially harmful temperatures of surface waters. The minimum effective temperature for movement is approximately 12.0 C. On winter days, box turtles are often active despite low air temperatures, with diurnal activity following ambient water temperatures more closely than air temperatures. Nearly all turtles may be forced to undergo temporary states of inactivity at night to avoid the cold from December through February.

15. Within marshes, 41 movements between successive points of capture were measured for 31 individuals; the mean straight-line distance was 12.8 m. Considered as an average home range radius, the mean diameter of the home range is 25.6 m. Box turtles seldom move in a direct line, but change directions and turn frequently, following a web-like system of shallow rivulets within marshes. Individuals seem socially tolerant of one another in nature and were often found foraging close together. No aggressive encounters were observed in the field, and there is no evidence of active territorial defense. Most _T_. _coahuila_ are sedentary, remaining within a given marsh for relatively long periods, but 21% of recaptured turtles had moved from one marsh to another, often over stretches of barren ground. Inter-marsh

distances traveled averaged 74 m.

16. Through July 1966, 164 adult or subadult T. coahuila of known sex were captured in the field; the sex ratio was 1.00 male / 1.34 females, not significantly different from a 1:1 ratio. A close correspondence in size of field-caught turtles with that of sexually mature individuals examined in the laboratory indicated that nearly all turtles recorded in the field were sexually mature or were approaching maturity. Only three juveniles were found, comprising less than 2% of the sample. Cryptic coloration and small size of young turtles makes them more difficult to obtain.

17. In the main study area, 114 T. coahuila were captued a total of 203 times. Slightly less than half of the individuals were recaptured at least once. An adverse effect on the behavior of marked box turtles occurred in the field, and in most marshes turtle activity seemed to decline markedly after several successive days of capturing turtles. Individuals were generally less susceptible to second and third captures, but were significantly prone to be captured four or more times.

18. Three census techniques were used to estimate the population size in the main study area: the single census, or Lincoln Index; the Hayne method; and the Schnabel multiple census. Numbers calculated using each method ranged

from 146 to 171 individuals in 11 regularly-sampled marshes in the study area. The total area of these marshes is 2.72 acres, so population densities ranged from 54 to 63 turtles per acre (1.3 to 1.6 turtles per are). Sixty turtles per acre probably represents a typical population density in most small marshes in the basin. Coahuilan box turtles are the largest and most noticeable element of the reptilian fauna living in many of the small, spring-fed marsh communities in the Cuatro Ciénegas basin.

19. Some *T. coahuila* possess compact deposits of algae and marl on the carapace. Among samples taken from carapaces of five individuals, six blue-green genera were identified, of which *Gloeothece* sp. and *Pleurocapsa* sp. were most common. With the exception of one unidentified blue-green alga, all genera lacked holdfasts and appeared to be on turtle shells largely by chance. Seven *T. coahuila* in the field harbored 1 to 4 small leeches (Hirudinea) on the skin or shell. Internally, about 45% of *T. coahuila* had small nematode worms in the stomach or intestine. Injuries most commonly observed in about 11% of turtles in the field were burn scars, limb amputations, and scars on the shell attributable to predators. Mortality is caused, in part, by man-set fires and by predators. The coyote, *Canis latrans*, has been implicated as one of the latter.

20. Coahuilan box turtles are remarkably agile swimmers

in relatively deep water of sinkholes, or posas, into which they occasionally enter, and they can easily elude human capture in such situations. In marshes, they are wary and rely mainly on escape by rapidly digging into the mud substrate for defense. When handled, all turtles closed their shells tightly so that soft parts were protected.

21. Populations of _T_. _coahuila_ in the marshes are relatively dense and the species may be able to withstand some diminishing of its numbers. Destruction of its habitat by a lowering of the water table through artificial draining clearly represents the main threat to the species. But because of voracious interest by curiosity-seekers, in rare animals whose habits and adaptations are so unusual, the existence of _T_. _coahuila_ could also be threatened by over-collecting. Future collections of the Coahuilan Box Turtle should be made only by investigators with a specific problem concerning the species.

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BIOGRAPHICAL SKETCH

William Sandwith Brown was born in West Chester, Pennsylvania, on September 3, 1941. He received part of his elementary and secondary education in the Downingtown, Pennsylvania Public Schools. In 1959 he graduated from Westtown School, Westtown, Pennsylvania, and entered Guilford College, Greensboro, North Carolina, later transferring in 1961 to Arizona State University, Tempe, Arizona, where he graduated in 1964 with a Bachelor of Science degree in Wildlife Biology. In September 1964 he was awarded a graduate teaching assistantship in the Department of Zoology at the Arizona State University, where he remained until May 1966 studying for the degree of Master of Science. In September 1966 he entered the University of Texas, Austin, Texas, to commence graduate studies for the Doctor of Philosophy degree while completing the research and the writing of this thesis begun in June 1965. He is a member of the Herpetologists' League and the American Society of Ichthyologists and Herpetologists.

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