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ECOLOGY OF THE AQUATIC BOX TURTLE,
TERRAPENE COAHUILA (CHELONIA, EMYDIDAE)
IN NORTHERN MEXICO

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GAINESVILLE

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ECOLOGY OF THE AQUATIC BOX TURTLE, *TERRAPENE COAHUILA* (CHELONIA, EMYDIDAE), IN NORTHERN MÉXICO

WILLIAM S. BROWN¹

SYNOPSIS: An ecological study of the Coahuilan Box Turtle, *Terrapene coahuila*, was undertaken between December 1964 and November 1967 in its natural habitat on the northern Mexican Plateau. The species is endemic to an intermontane basin of the Chihuahuan Desert near Cuatro Ciénegas, Coahuila. Its geographic range consists of disjunct populations in an area that does not exceed 800 km².

Preferred habitats of *T. coahuila* in the area studied are small, north-south trending, spring-fed marshes, characterized by mud bottoms, shallow water, and dense aquatic vegetation, principally *Chara* spp., *Eleocharis rostellata*, and *Scirpus olneyi*. Marshes are distinct aquatic communities surrounded by desert grassland and shrub communities.

Ecological adaptations of this species more closely resemble those of other North American aquatic turtles than of terrestrial members of its own genus. Population densities, foraging behavior, food habits, and thermal relationships best exemplify the aquatic mode of life of *T. coahuila*.

T. coahuila remains active throughout the year except for short periods of environmental extremes. Mating occurs from September to June and appears concentrated in spring. Copulating pairs of box turtles were found in October, November, December, and April, frequently in shallow water. The ovarian cycle appears to be intermediate between the lengthy cycle of tropical emydid species and the compressed cycle of northern species caused by cold weather. Follicle enlargement occurs between late August and early April when ovulation begins. Egg laying begins in May and continues to September. Complements of 2 or 3 eggs are produced most frequently. An estimated half of the females can produce second clutches, and about one-third may deposit three sets annually. These females produce a mean of 6.8 eggs/female per season, a higher reproductive potential than in certain northern populations of *Terrapene*.

Coahuilan box turtles forage in shallow water, with the carapace usually above the surface and dry, and the head extended underwater. *T. coahuila* is opportunistic

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and omnivorous, feeding extensively on aquatic plants (*Eleocharis*) and insects (stratiomyid fly larvae, beetles, hemipterans, dragonfly nymphs). Foraging behavior and food habits of *T. coahuila* are comparable to other aquatic or semiaquatic emydids (*Chrysemys picta*, *Clemmys muhlenbergi*).

Cloacal temperatures of *T. coahuila* active in marshes closely approximate water temperatures at all seasons, as is generally true for most other aquatic turtles while in water. There is wide seasonal and daily variation in the mean cloacal temperature of active turtles, so no single optimum temperature within the activity range is reported.

In summer, when water temperatures can exceed tolerable levels, activity occurs mainly in early morning, late afternoon, and at night. Marsh bottoms provide a cool refuge into which a turtle can burrow to avoid potentially harmful midday surface temperatures. Most *T. coahuila* presumably undergo temporary states of winter inactivity, although some remain active in water despite low air temperatures. In December, when several individuals on land had cloacal temperatures elevated well above air temperatures, basking was indicated.

Most *T. coahuila* remain within a given marsh for relatively long periods, but about 20% of recaptured turtles had moved longer distances, possibly overland, from one marsh to another. Within marshes, movements between successive points of capture averaged about 13 m. Box turtles move in a sinuous fashion over mats of *Chara* and around sedge tussocks. Individuals seemed socially tolerant of others in nature, and were occasionally close together; no aggressive encounters were observed.

Three mark-recapture census techniques were used to estimate the population size in the study area. Population densities ranged from 54 to 63 adult turtles per marsh acre (133-156/ha). *T. coahuila* occurs in relatively higher numbers and is restricted to smaller areas of activity than its terrestrial congeners, *T. carolina* and *T. ornata*. Its population density is more comparable to certain aquatic species, such as *Chrysemys picta* and *Pseudemys scripta*.

Although populations of the Coahuilan Box Turtle are relatively dense in many marsh communities in the Cuatro Ciénegas basin, *T. coahuila* can be considered a rare species by virtue of its restricted aquatic habitat. Destruction of marshes by draining and excessive collecting of specimens clearly represents threats to the turtle's existence. *Terrapene coahuila* should be obtained, therefore, only by those seriously investigating its biology.

TABLE OF CONTENTS

INTRODUCTION	3
ACKNOWLEDGEMENTS	4
METHODS	4
GEOGRAPHICAL SETTING AND HABITAT	5
Study Area	6
REPRODUCTION	11
Mating	11
Sexual Maturity and Seasonal Changes in Males	14
Sexual Maturity and Seasonal Changes in Females	16
Reproductive Potential	20
Egg-laying Season	24
Eggs	26
GROWTH	26
BIOTIC ASSOCIATES	28
INJURIES AND PREDATION	29
THERMAL RELATIONSHIPS	31
Activity Temperature	31
Daily and Seasonal Activity	37
FOOD AND FEEDING	39
Foraging Behavior	39
Diet	41
MOVEMENTS	48
POPULATION	51
Composition	51
Density	54
Mortality and Replacement	59
SOCIAL RELATIONSHIPS	60
SURVIVAL STATUS	61
LITERATURE CITED	62

INTRODUCTION

Turtles of the family Emydidae are the most nearly cosmopolitan and generalized of living chelonians. Most emydids are aquatic or semi-aquatic, but some genera have evolved terrestrial adaptations. One such North American group is the terrestrial genus *Terrapene*, the widely distributed and familiar box turtles, of which 4 species and 11 subspecies are recognized (Milstead and Tinkle 1967). One species, *Terrapene coahuila*, is exceptional among living members of the genus in that it alone is aquatic.

Terrapene coahuila is restricted to a semi-isolated intermontane desert basin of about 800 km² lying generally south of the town of Cuatro Ciénegas, Coahuila, in northern México. The Coahuilan box turtle occurs principally in marshes of the Cuatro Ciénegas basin, though other aquatic habitats occur there (Minckley 1969).

Since the description of *Terrapene coahuila* by Schmidt and Owens (1944), habitats, habits, and distribution of the species were surveyed

by Webb, Minckley, and Craddock (1963). Data concerning food, reproduction, and populations were lacking.

As the turtle is ecologically and evolutionarily unique in the genus (Milstead 1969; Brown 1971), it seemed pertinent to investigate its ecology and compare this information with that of aquatic emydids and with the terrestrial *Terrapene*. This paper reports the results of a field study conducted on 87 days between December 1964 and November 1967. Heaviest concentration of work in México was in July and August 1965.

ACKNOWLEDGMENTS

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I especially want to thank the people of Cuatro Ciénegas de Carranza, whose friendship and warm hospitality made my stay most pleasant. I express my sincere gratitude to José Lugo Guajardo and Catalina Díaz de Leon de Lugo for their enthusiastic aid and encouragement. I am indebted to former Presidente Municipal of Cuatro Ciénegas, Francisco Manrique Dávila, and to his successor in that office, Victor Castillo Soto, for official clearance and introductions. Generous thanks are also given to Modesto B. de la Garza Palos, Gines Nilo de la Garza Palos, Dr. Rodolfo Castro Villarreal, Manuel González Verduzco, José Ibarra González, Armando Moncada Rivas, and many others for numerous courtesies.

METHODS

T. coahuila were hand-collected and marked by notching the marginal scutes of the carapace. Movements were studied by capture and release. Points of capture were plotted on maps of the study area. Maps of individual marshes were prepared from field measurements obtained with a surveying transit. A total of 169 *T. coahuila* was marked; 36% of these were recaptured a total of 271 times. The following data were recorded for each individual captured: general weather conditions, cloacal and environmental temperatures, body measurements, presence of ectoparasites, injuries, and markings.

I examined 59 preserved specimens. Reproductive systems and digestive tracts of 48 specimens (14 males and 34 females) showed food habits and gonadal cycles in spring and summer. Reproductive systems only of seven females in autumn were inspected, for a total of 55 subadult or adult size individuals surveyed. Of these,

29 were collected in July and August 1965, 19 in April 1966, 6 in October 1967, and 1 in November 1967. They are deposited in the following collections: Arizona State University (ASU) 5853-5900, and University of Utah (UU) 12551-12557. Four additional preserved juvenile specimens examined for growth rings are from the following collections: United States National Museum (USNM) 159578; UU 3646; and ASU 8000-8001.

All mean values in this paper are followed by \pm one standard error (SE) of the mean.

GEOGRAPHICAL SETTING AND HABITAT

The Cuatro Ciénegas basin is in central Coahuila (Fig. 1) at the eastern edge of the Mesa del Norte, or Ridge and Basin Province, of northern México. The basin is an expansive plain nearly enclosed by mountain ranges of Cretaceous limestone (Minckley 1969), and lies within the Chihuahuan Desert faciation of the Hot Desert Biome (Muller 1947; Shelford 1963). Climate of Coahuila is influenced primarily by its continental position and its mountain ranges (Muller 1947). Most of the state is arid, with an annual rainfall of 0 to 200 mm (Shreve 1944; Vivó Escoto 1964).

Elevation of the basin floor is about 740 m above sea level; surrounding mountains are generally between 1500 and 3000 m high (Minckley 1969). Three passes into the basin sequentially break the eastern-bounding Sierra del Carmen—Sierra Madre Oriental axis, or Coahuila Folded Belt (West 1964), and connect the lowland Gulf Coastal Plain with the Mexican Plateau. External draining of some of the basin's waters through these gaps is by canals to the Río Salado de los Nadadores in the drainage system of the Río Grande.

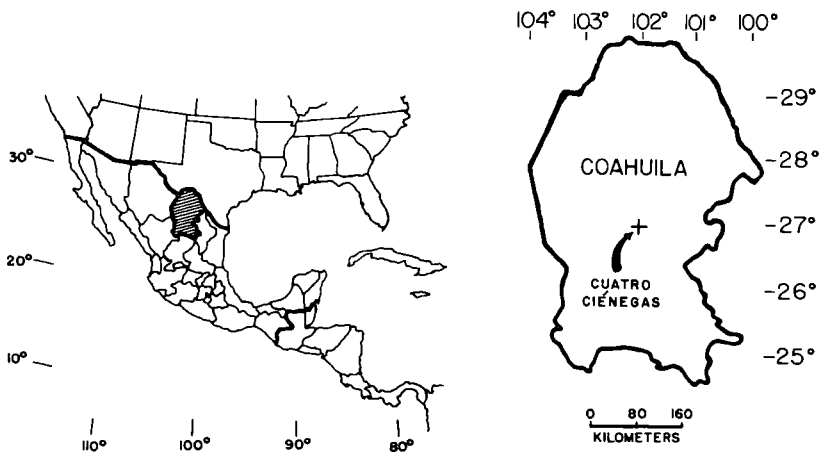


FIGURE 1.—Geographical location of Cuatro Ciénegas, Coahuila, México.

This small (ca. 30 x 40 km) intermontane bolsón lies just inside the Chihuahua-Zacatecas Biotic Province near its zone of contact with the Tamaulipan Biotic Province to the east (Goldman and Moore 1945; Stuart 1964). Innumerable springs, marshes, rivers, and ponds, many of which are parts of distinct internal drainages, contribute to the biological diversity of the Cuatro Ciénegas basin.

High endemism exists among the snails, crustaceans, and fishes (Minckley 1969). Three of the four taxa of turtles known from the basin are endemic. In addition to *T. coahuila*, basin endemics are *Pseudemys scripta taylori* (Legler 1960a) and *Trionyx ater* (Webb and Legler 1960). *Trionyx spiniferus emoryi*, the fourth taxon, occurs widely in southwestern U. S. and northern México, including the Cuatro Ciénegas basin (Webb 1962; Winokur 1968).

STUDY AREA.—A site approximately 9.5 km almost due southwest of the town of Cuatro Ciénegas was chosen for intensive field work (Fig. 2). It is a gently-sloping grass zone immediately below the rock pediment (bajada) of the northeast tip of Sierra de San Marcos, extending finger-like into the basin from the south.

To the west and east around Sierra de San Marcos, many springs and marshes lie immediately downslope from the bajada of the mountain. *Terrapene coahuila* is perhaps more plentiful in this region of extensive marshes than in other more widely-scattered areas of suitable habitat within its limited range (Fig. 2).

Transition from the rocky bajada to the grassy flats of the basin floor (barrial) is abrupt. Here, the soil is bleached and fine-textured, often becoming soft and spongy after a rain. Halophytic grasses, particularly *Distichlis* spp., are prominent in the study area. Patches of iodine bush, *Allenrolfea occidentalis*, are abundant. Stands of marsh grass, *Spartina spartinae*, and alkali sacaton, *Sporobolus airoides*, are less extensive. Bare regions, sparsely covered with scattered clumps of mesquite (*Prosopis juliflora*), catclaw (*Acacia greggii*), inkweed (*Suaeda fruticosa*), and *Allenrolfea*, are occasionally encountered within the farther-ranging *Distichlis* flats.

Near moist, spring-fed drainages, slight local subsidence of the basin floor is evident. All marshes are characterized by spike-rush, *Eleocharis rostellata*, approximately 50–70 cm tall. This sedge provides most (ca. 70%) of the vegetative cover, but is supplemented in many marshes by thick, submersed mats of stonewort, *Chara* spp. Bullrushes, *Scirpus olneyi*, are prominent sedges in several marshes (Fig. 3A). In others, *Scirpus* is dispersed without noticeable zonation among the more abundant *Eleocharis*.

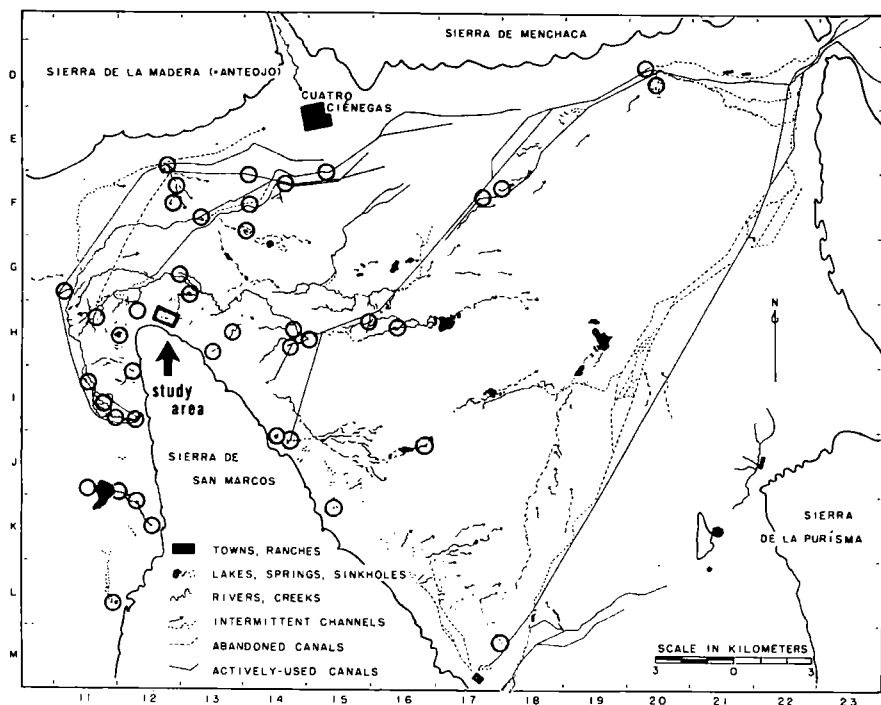


FIGURE 2.—Distribution of *T. coahuila* in the Cuatro Ciénegas basin as shown by known sites of collection or sight records, 1958 to 1968 (W. L. Minckley, unpublished). Map (provided by W. L. Minckley) is arranged with an approximately 2.5 km grid, letters designating N-S sections, numbers designating E-W sections. Precise grid locations are indicated by subdivision of the square sections (e.g., study area is in NE1/4, H-12). For place names of localities see gazetteer in Minckley (1969).

Among other plant species that occur frequently in and around the marshes or grow near them, seep-willow, *Baccharis glutinosa*, commonly fringes a marsh, usually along the northern border. Of the 11 marshes in the area of intensive study, 7 had conspicuous clumps of *Baccharis* along them (Fig. 3B). The sedge, *Fimbristylis thermalis*, sawgrass, *Cladium californicum*, and cattails, *Typha* spp., are less common plants of the marshes. *Distichlis stricta* is usually found near moist spots close to a drainage channel or a marsh, and occasionally occurs on raised patches within a marsh.

The distinctness of the marshes from surrounding halophytic grass communities is readily apparent. Marsh borders end abruptly as they meet the dry, or seasonally water-logged, saline soil of the barrial.

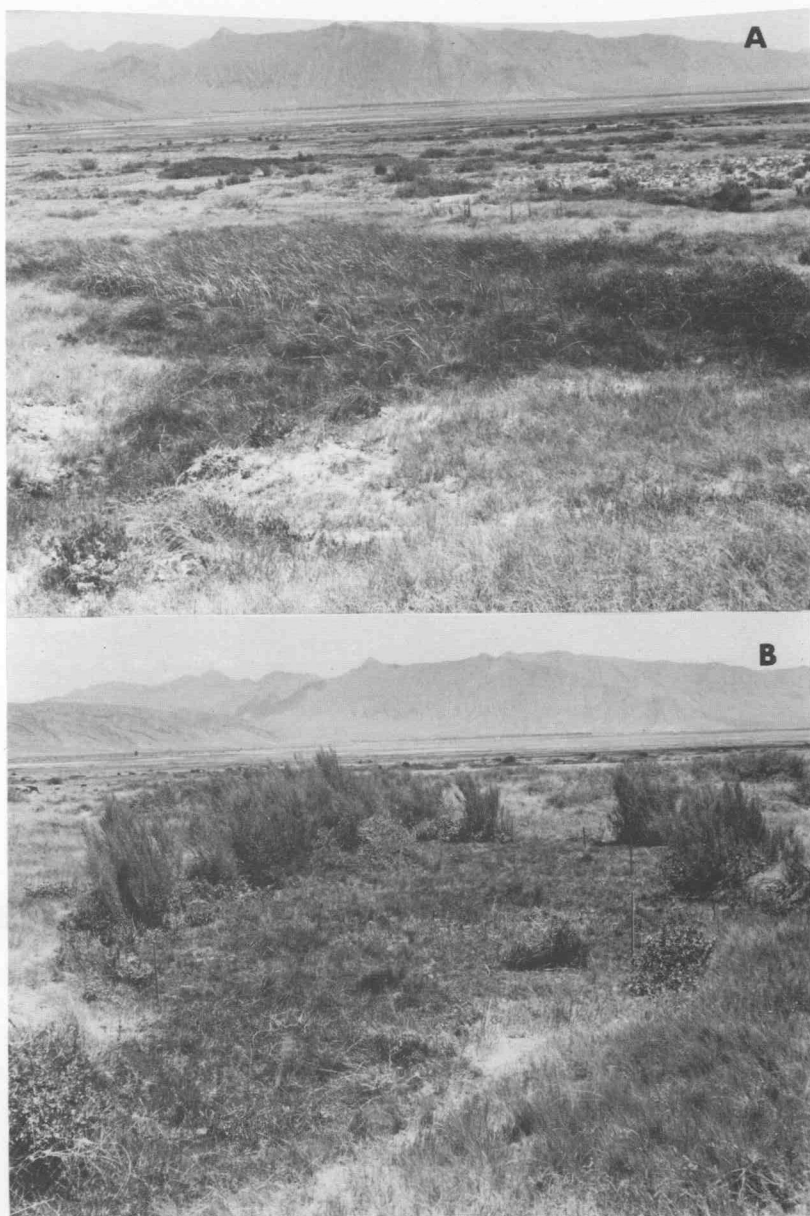


FIGURE 3.—Marsh habitat of *T. coahuila*, 28 July 1965, views northeast. Grasses surrounding the marshes are largely *Distichlis* spp. A. Marsh 2-A; vegetation is mainly *Scirpus olneyi* and *Eleocharis rostellata*, with scattered *Spartina spartinae* and *Cladium californicum* at north end of marsh. B. Marsh 5; vegetation is mainly *Eleocharis rostellata* with *Baccharis glutinosa* prominent around edges. (Stakes around marsh perimeter were for mapping purposes.)

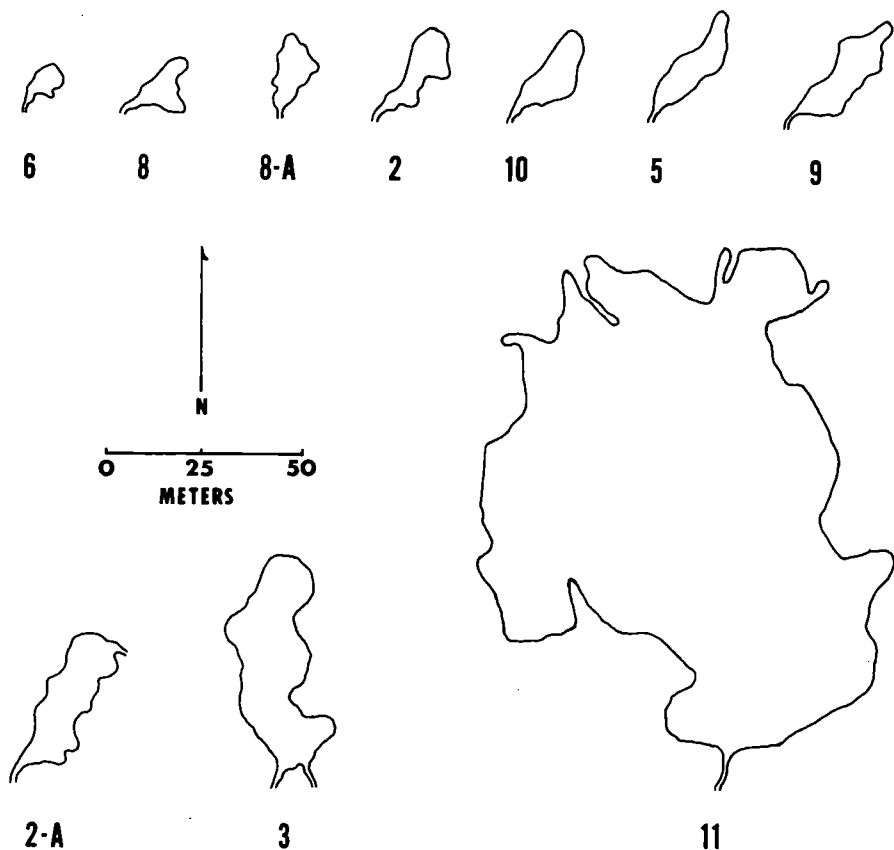


FIGURE 4.—Outline maps of 10 marshes in the study area. Marshes are arranged from smallest (left) to largest (right).

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 were mapped (Fig. 4) and their areas were determined by means of a planimeter (Table 1). Lengths ranged from 13 to 130 m, and widths from 7 to 100 m. Excluding the largest marsh (no. 11, which was more than 150 times larger in area than the smallest), maximum dimensions averaged 30 x 12 m.

All marshes studied receive water directly or indirectly from a number of springs and narrow stream channels entering from the south. All are oriented with their long axes in a general south-north direction. Flow is north and northeast toward El Mojaral, a series of several large ponds (lagunas) about a kilometer north of the study area. One stream approximately a meter wide carries the greatest volume of water of those in the study area.

TABLE 1. SIZES OF 11 MARSHES IN THE STUDY AREA.¹

Marsh No.	Area	
	m ²	Acres
11	8,745	2.16
3	751	0.18
2-A	394	0.10
9	234	0.06
5	186	0.05
10	172	0.04
2	157	0.04
8-A	118	0.03
8	104	0.03
1	102	0.02
6	56	0.01
Total Area	11,019	2.72

¹ Areas of all except Marsh 1 (area estimated) were determined with a planimeter.

The channels tend to widen imperceptibly near a seep, or marsh, then become braided. Within a marsh flow is reduced 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. During July and August 1965 the surface water in several marshes evaporated during the day, exposing patches of wet mud, but water was always replenished overnight. No marsh in the study area dried completely.

Two marshes (8A and 3) had small, underground exit tubes along their northeast borders, where water flowed out in small streams about 10 cm wide. Subterranean channels were further evidenced by several small (50 cm diameter) sinkholes in the grassy terrain between marshes. No surface channels connected one marsh with another, with one exception: marshes 8 and 8A. Marshes 9, 3, and 11 received their water by surface streams directly from nearly circular, spring-fed pits (posos), approximately 4 to 6 m in diameter (Fig. 5).

Much of the study area, especially the intervening grass zones outside the marshes, is periodically burned by man. Burned areas were locally extensive, but did not cover more than a few hundred or perhaps a few thousand m². Charred grass tussocks and young second-growth plants evidenced old and recent fires over much of the area. Fires did not appear to kill larger shrubs, such as mesquite or acacia, and did not seem to cause long-term damage to marsh vegetation. During winter when vegetation is dry, some large marshes of the basin are occasionally destroyed by fires.



FIGURE 5.—Poso, or small spring-fed pool, in study area, 31 July 1965. Water temperature at all seasons averaged 33.5°C in this sinkhole, typical of those in which *T. coahuila* occasionally forage.

Herds of 5 to 15 horses and mules grazed in and around the marshes almost daily during July and August 1965. They seemed to relish *Eleocharis*, and thus often diminished the cover this sedge normally provided the box turtles. Horses had severely grazed 7 of the 10 smaller marshes. An occasional transient herd of goats entered the study tract, but these usually did not remain longer than an hour and caused no observable damage.

REPRODUCTION

MATING.—Approximately 30 Coahuilan box turtles have been maintained in an artificial outdoor pond at Arizona State University, Tempe, and several of these attempted to mate. The pond is roughly circular, about 8×10 m. About half of it is shallow (ca. 1–20 cm) and half deep (ca. 1 m). In April 1966 I saw a male mounted on a female in relatively deep (ca. 25 cm) water in this pond. The male's rear claws gripped the female's posterior, apparently on the skin of the gluteal region, and he snapped at the female's head. The female was completely submerged and made vigorous 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.

W. L. Minckley saw copulations between captive *T. coahuila* in the artificial pond on 10 dates between 16 September 1965 and 11 June 1966. No matings were recorded in October, January, and February. Minckley saw two different copulating pairs on 4 March 1966 at 7:40 AM, and three pairs on the mornings of 17 March 1966. 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 a male followed a female with his 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. Two copulations were timed at approximately 2 hours, and 2 hours and 20 minutes (W. L. Minckley, unpublished).

The first of three phases of mating in *T. carolina* observed by Evans (1953, 1968) consisted of the male pushing, circling, and biting at the female's carapace and striking it with the anterior portion of his plastron. The entire courtship of *T. carolina* lasted up to 6 hours with up to 2 hours in copulation (Evans 1953). Brumwell (1940) recorded a 30-minute copulation time in *T. ornata* and saw a male of that species striking the carapace of a female with his plastron and biting at her carapace before mounting.

Copulating pairs of *T. coahuila* were found several times under natural conditions. On 31 December 1964 at midday, a pair was discovered at the edge of a dense growth of *Baccharis* along the edge of a marsh in the 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.

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 2 hours earlier, but the study area received only a trace. Weather was clear and humid, air temperature 29.0°C. Water temperature near the marsh inlet was 22.6°C. Both turtles were in shallow (2-5 cm) water. The male

was lying on his carapace and was being dragged slowly by the female. When disturbed they separated and 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.

On 20 October 1967 at 11:30 AM in marsh 8, a pair of marked *T. coahuila* was copulating in water ca. 10 cm deep. The male made rapid movements above the submerged female. Water temperature was 29.2°C, and air approximately 23.0°C. A month later, on 21 November, another pair of marked individuals was copulating in shallow water of a localized spring overflow among *Distichlis* grass near marsh 5 at 2:30 PM. Air temperature was approximately 29°C. The animals were discovered after I heard their shells striking sharply together. The male was on his back immediately behind the female.

Cahn and Conder (1932) and Evans (1953, 1968) described copulation in captive *T. 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. Secured by the hind legs of the female, the male leans back and effects coitus. Legler (1960b) states that coitus of *T. carolina* differs from that of *T. ornata* in the position of the male's legs. It seems necessary for male *Terrapene* to tilt backward to achieve effective copulation, perhaps because of their relatively short tails and high-domed shells.

Legler, in Webb et al. (1963), noted that a female *T. coahuila* was drowned by a male during mating in an aquarium. Females probably rarely drown while mating in the shallow water of marshes, but may do so in the deeper water of sinkholes or pools. Few turtles were seen in such habitats in the study area, and no mating turtles were noted in pools along the Río Mesquites (Fig. 6).

Mating in *T. carolina* and *T. ornata* takes place in the spring after emergence from hibernation and less frequently in the fall prior to hibernation (Ewing 1933, 1935; Allard 1935; Rosenberger 1936). It has been reported to occur sporadically throughout the season of activity, approximately from April to October in Washington, D.C. for *T. c. carolina* (Allard 1935, 1949), and from mid-April to late October for *T. o. ornata* in Kansas (Legler 1960b). Penn and Pottharst (1940) noted that *T. carolina major* in New Orleans, La. mated most often after a rain or when temperatures were between 21.1° and 26.7°C. Twice mating occurred in water.

The records of November and December matings by *T. coahuila* in nature suggest extended, perhaps nearly year-round, sexual activity of at least part of the population. Studies of captive and wild *T. coahuila*



FIGURE 6.—Two *Terrapene coahuila* (indicated by arrows) foraging in pools along Río Mesquites, ca. 7.5 km SW of Cuatro Ciénegas, 30 July 1965. Water temperature 33°C. Note dense sedge cover.

showed mating is frequent from September to June and most common in March and April. No matings were recorded during July and August 1965, the period of most intensive field work.

SEXUAL MATURITY AND SEASONAL CHANGES IN MALES.—Measurements and weights of testes were determined with vernier calipers and triple-beam balance. Testes volumes were determined by water displacement. Epididymal smears from each male and several smears of gonadal tissue were examined microscopically for the presence of sperm.

Of 14 males dissected 10 had sperm in the epididymides and were considered to be sexually mature (mean carapace length, 109.5 ± 2.2 mm). Based on this sample, 95% confidence limits indicate that carapace lengths of mature males 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 (1960b) 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 young specimens, but are somewhat greater than carapace lengths in mature animals.

A few sperm were present in the epididymides of four *T. coahuila*

with small testes in late July and August. In 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 were clearly subadult and probably immature (carapace lengths 85.1 and 89.2 mm), whereas two collected in the last week of July appeared to be adults on the basis of size (117.2 and 131.5 mm) and external appearance. Testes of the last two contained no sperm and were very small, with combined weights of trace and 0.08 g and volume displacements of 0.01 and 0.12 ml, respectively. Two additional adult-sized males (testes 0.07 and 0.15 g; 0.08 and 0.18 ml) caught at about the same time (26 July) had sperm in their epididymides. These individual differences may be explained by prior expenditures of sperm toward the end of the spring-early summer mating period at a time when the ensuing spermatogenic cycle may well be in its early stages before new sperm have matured. Mature spermatozoa were found in the epididymides of *T. c. carolina* throughout the year (Altland 1951) and in *T. o. ornata* throughout the activity season (Legler 1960b). Tinkle (1958b) discovered no sperm in the testes of 20 large male *Sternotherus carinatus* and concluded that they were "out of season" when collected, commenting: "The complete absence of spermatozoa was unusual, as a few generally may be found even in out of season males of other forms." Moll and Legler (1971) noted the presence of some epididymal sperm in *Pseudemys scripta* from Panamá in all months, with fewest numbers occurring in June and July.

Seasonal changes in testis 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 (Risley 1938; Altland 1951; Gibbons 1968c). Fluctuation in testis size is evident in *T. coahuila* (Table 2). The testes were small in specimens from April and July, but had increased dramatically by late August in two of four specimens. Available data on testis size and relative abundance of sperm indicate a spermatogenic cycle not greatly different from the north temperate pattern for turtles in which spermatogenesis takes place in summer and mature sperm overwinter in the sex accessories (Miller 1959; Moll and Legler 1971).

On the basis of observed matings of *T. coahuila* in nature and under semi-natural conditions, and because of its habitat in a southern, thermal-spring environment which permits a more extended period of sexual

TABLE 2. TESTIS SIZES OF 10 MATURE MALE *T. coahuila*.

Month	Mean Testis Diameter (mm)	Mean Weight of Both Testes (g)	Mean Volume of Both Testes (ml)
April (n = 4)	6.4 (5.0-9.0) ¹	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)

¹Ranges in parentheses.

activity than in more northern turtles, spermatogenesis may be extended longer into the winter, as in Panamanian *Pseudemys scripta* (Moll and Legler 1971). If this occurs, *T. coahuila* has a spermatogenic cycle differing in extent from the known cycle of *Sternotherus odoratus* (Risley 1938), *Chrysemys picta* (Gibbons 1968c; Ernst 1971a), and the two U. S. species of *Terrapene* (Altland 1951; Legler 1960b). Comparative data are lacking for *T. carolina* populations of southeastern México and *T. nelsoni* of western México.

SEXUAL MATURITY AND SEASONAL CHANGES IN FEMALES.—Ovaries and oviducts of preserved 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. Ovaries and eggs were weighed after being trimmed of connective tissue and blotted with an absorbent paper towel. The condition and relative size of oviducts were noted.

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 were also used to indicate sexual maturity, especially in postre-productive 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.

Carapace lengths of 30 mature females ranged from 90.7 to 147.5 mm, mean 101.6 ± 2.1 mm. Based on this sample, 95% confidence limits indicate that carapace lengths 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 (1960b) had a plastron length of 107 mm; 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. Males became sexually mature at a smaller size than females. In *T. coahuila* this situation is re-

TABLE 3. OVARIAN WEIGHTS AND NUMBERS OF FOLLICLES IN OVARIES OF 30 MATURE FEMALE *T. coahuila*.

Month	Mean Weight of Both Ovaries (g)	Mean Number of 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)

versed: sexually mature females were significantly ($P < 0.05$) smaller than males.

The spring and summer samples examined contained 15 female *T. coahuila* taken in the first week of April 1966, 10 in July 1965, and 9 in August 1965. July and August individuals did not differ in condition of their reproductive tracts and were combined. Seasonal comparisons were made between the April (spring) and the July-August (summer) group. Two individuals from each sample were considered subadult or immature, reducing the numbers to 13 mature females in April and 17 in July and August. Although carapace lengths of mature females in the summer sample averaged slightly larger (103.4 mm) than those in the spring sample (99.2 mm), there was no significant difference in size between the two groups ($P > 0.30$). Follicles were arbitrarily grouped into size classes as follows: 1–4 mm, 5–9 mm, 10–14 mm, and >15 mm.

In spring all 13 mature females were prereproductive and had not yet ovulated. These had heavier ovaries than females in summer (Table 3), but the difference between them was not statistically significant ($P > 0.10$). Weights of preserved ovaries of *T. coahuila* were considerably less than those of *T. c. carolina* (Altland 1951) and *T. o. ornata* (Legler 1960b). Ovarian weights of *T. coahuila* early in July tended to be greater than those in late July and August.

There was no correlation between an adult turtle's size and the total number of follicles greater than 2 mm in the ovaries in both the spring sample ($P > 0.05$) and the summer sample ($P > 0.05$). Females in summer had a significantly greater ($P = 0.01$) mean number of follicles per female than did the spring females (Table 3). Most of these were small follicles, indicating that most of the turtles in the July-August sample were postreproductive, in a period between a previous ovulation and the beginning of a new ovarian cycle. Legler (1960b) reported the formation of many small follicles in the ovaries of female *T. ornata* in July or August.

Figure 7 shows the distribution of follicle sizes in all mature females from both samples; 44 percent more females in spring than in summer

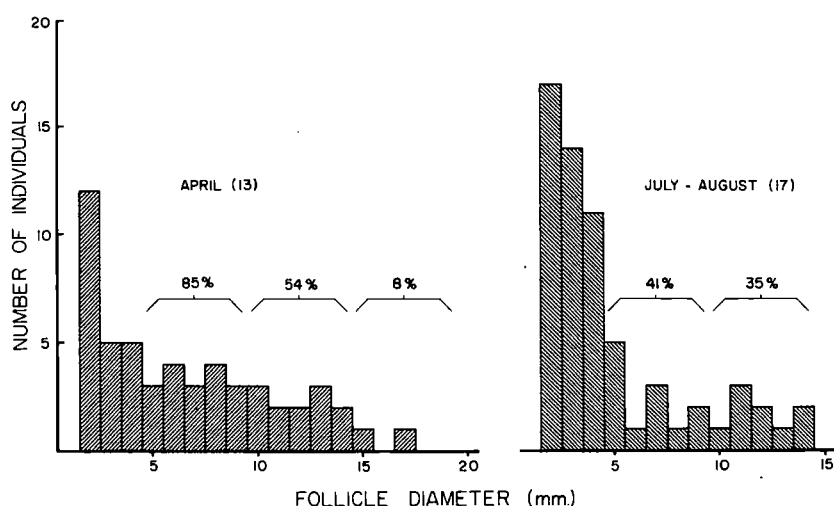


TABLE 4. SIZE RANGES OF OVARIAN FOLLICLES IN SEVEN FEMALE *T. coahuila* (UU 12551-12557) IN AUTUMN 1967.¹

Date of Collection	Enlarged Follicles	Small Follicles
2 October	5.2-5.6 (2)	3.9-4.2 (3)
"	7.2 (1)	3.6 (1)
"	4.6 (1)	3.3-4.1 (6)
18 October	7.1-9.1 (5)	(0)
"	(0)	2.5-4.0 (8)
20 October	(0)	3.0-4.0 (4)
12 November	5.7-7.2 (2)	3.2 (1)

¹ Measurements in mm; number of follicles in parentheses.

could have been ovulated later that season, or they may have been held over until the following spring.

In autumn seven mature females had a total of 34 follicles >2 mm. Mean size of the follicles was 4.6 mm (range 2.5-9.1). Of these, 11 (32%) were in the 5-9 mm size range and occurred in five of the seven females (Table 4). Enlarged follicles in this small autumn sample averaged 6.9 mm. No corpora lutea were discernible macroscopically.

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 (Tables 3 and 4, Fig. 7). Follicles of females that deposit clutches in late summer may undergo enlargement in late winter and the following spring.

Follicular atresia in *T. coahuila* is not great. Only two slightly enlarged, 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 (1960b) observed brown, orange, or purplish atretic follicles in ovaries of "many" female *T. o. ornata*.

Ovaries of *T. c. carolina* were heaviest in May when they contained 2 to 8 enlarged follicles (Altland 1951). Ovulation usually occurred in June and July with a corresponding decrease in ovarian weight, but ovulation could occur as late as August 15. Follicles began to enlarge in July and August, following ovulation. Altland suggested that some of the enlarged follicles formed prior to hibernation were held over to the next reproductive season. Likewise, follicles of *Chrysemys picta* in Pennsylvania remained in an enlarged, quiescent state through winter

after a period of postovulatory summer growth (Ernst 1971a). The ovarian cycle of *T. ornata* (Legler 1960b) is similar to that of *T. carolina*. Ovaries weighed most in March and April prior to initial ovulation during May and June; an estimated 33% of females were capable of a second ovulation in July. The cycle began in late summer, ovarian weights increasing in October before hibernation.

Essentially the same timing occurs in ovarian cycles of northern temperate aquatic turtles that have been studied (*Chrysemys picta*, Powell 1967; Gibbons 1968c; Ernst 1971a; *Sternotherus odoratus*, Risley 1933). Moll and Legler (1971) studied the ovarian cycle of a tropical aquatic species, *Pseudemys scripta*, in Panamá and found that ovulation occurred in the first half of the calendar year (December to May), and oviposition was completed by August. Follicles began to enlarge again in the last half of the year following a quiescent period in July and August.

Except for a several-month period of interruption imposed by cold weather and resulting hibernation in northern species, similar patterns of timing occur in temperate as well as certain tropical emydid turtle species known to date. In the Cuatro Ciénegas basin, low temperatures during an estimated 3-month period from December through February (see "Seasonal Activity") may inactivate box turtles. Although the *T. coahuila* population apparently does not undergo any sustained period of hibernation, cool weather probably delays completion of follicular enlargement and ovulation until around April. Ovulation can seemingly continue into August and oviposition into early September (see below). The ovarian cycle of *T. coahuila* appears to be intermediate between the lengthy cycle of tropical species and the shorter cycle of northern species compressed by cool weather.

REPRODUCTIVE POTENTIAL.—Studies of 16 female *T. coahuila* (6 with large preovulatory follicles, 7 with corpora lutea or enlarged follicles or both, and 3 with oviducal eggs or enlarged follicles or both) representing 23 potential clutches indicate that complements of 2 or 3 eggs are produced most frequently (Fig. 8), with an over-all mean clutch size of 2.3 (range 1 to 4).

Mean clutch size for *T. c. carolina* near Washington, D.C., has been reported as 4.2, 3.0, and 3.6 eggs (Ewing 1933, 1935; Allard 1935). Altland (1951) recorded 2 to 5 eggs in *T. c. carolina* from Pennsylvania and Maryland. Legler (1960b) found 2 to 8 eggs (mean 4.7) in 23 clutches of *T. o. ornata* in Kansas. 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) gave a mean of 2.2 eggs in southern and 4.6 eggs in northern *Sterno-*

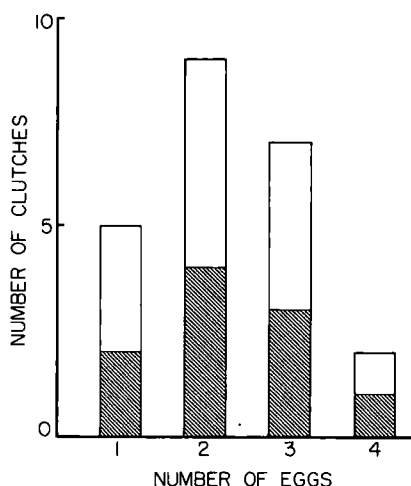


FIGURE 8.—Number of eggs in 23 clutches of *T. coahuila*. Shaded portions represent clutches determined from counts of oviducal eggs and corpora lutea; unshaded portions represent potential clutches determined from counts of enlarged ovarian follicles.

therus odoratus, and showed that clutch size in *S. odoratus* decreases progressively as one moves south to lower latitudes. Selective factors involved in this variation are discussed by Tinkle (1961) and Moll and Legler (1971). *Chrysemys picta* produce clutches averaging 8.5 eggs in Nova Scotia (Powell 1967), 6.6 in Michigan (Gibbons 1968c), 6.3 in Illinois, and 4.3 in Tennessee (Cagle 1954). Small clutch sizes (mean 2.7 eggs) of *Terrapene n. nelsoni* from Nayarit, México, reported by Milstead and Tinkle (1967), together with that reported here for *T. coahuila*, concur with Tinkle's (1961) data on *S. odoratus* and those available for *C. picta*, and suggest that latitudinal variation in clutch size also occurs in *Terrapene*. Whether this conclusion remains valid will ultimately depend on detailed work within a single geographic region to determine the extent of reproductive variability between local populations. Particularly, Gibbons and Tinkle (1969) have shown significant differences in clutch size between three closely situated populations of *Chrysemys picta* in Michigan.

Of 10 July and August female *T. coahuila*, 7 had corpora lutea in the ovaries but no oviducal eggs, indicating recent oviposition. In the three females with oviducal eggs (mean 3.0), corpora lutea were cuplike structures approximately 6 to 7 mm in diameter and appeared similar to the corpus luteum of *T. c. carolina* (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 recorded for other species by Legler (1958) and Tinkle (1959a), and no indication that any eggs had been laid before the turtle was preserved. Altland (1951) and Moll and Legler (1971) noted degeneration of corpora lutea in some female *T. c. carolina* and *Pseudemys scripta*, respectively, while eggs were still in the oviducts. Atresia of corpora lutea in *T. c. carolina* was completed by August, shortly after the egg-laying period. Corpora lutea of *T. o. ornata* underwent rapid involution and were barely discernible 2 to 3 weeks after oviposition (Legler 1960b).

A large female *T. coahuila* containing four oviducal eggs had both oviducts, each containing two eggs, displaced to opposite sides of the body cavity. This individual was the largest turtle of either sex taken (147.5 mm carapace length). Legler (1958) noted a similar phenomenon in *T. o. ornata* when oviducts contained large complements of eggs.

Six April females approaching their first ovulation of the season had 2 to 4 preovulatory follicles (mean 2.7). These follicles are thought to represent the first clutch. 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 April females also gave indications of multiple-clutch capability, containing five and six follicles greater than 5 mm in diameter that presumably represented two developing clutches.

Ovulation first occurs for most of the population in April with egg laying in May. An additional set of ova could be ovulated and deposited by June or early July. Ten females taken between 3 July and 24 August 1965 provide evidence for second and third clutches in *T. coahuila*. Of seven females with corpora lutea, four had 1 or 2 preovulatory follicles, and of 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. (One female with two oviducal eggs on 26 August 1965 is not included because it contained no enlarged follicles definitely indicating a second clutch.) All females in the population would probably not lay second clutches, as some individuals in the July-August sample had neither corpora lutea nor enlarged follicles. Rapid disappearance of corpora lutea, however, and collection of females

in an intermediate period may, as mentioned earlier, influence this conclusion. The six females (35% of July-August sample) believed capable of depositing third clutches contained from 1 to 3 preovulatory follicles (mean 1.7).

Multiple clutches in turtles are generally known (Legler 1960b). *Chrysemys picta* apparently produce two similar-sized clutches annually in Michigan (Gibbons 1968c), but only one in Pennsylvania (Ernst 1971a). Tropical *Pseudemys scripta* produce up to six clutches per season (Moll and Legler 1971). Approximately 33% of female *T. o. ornata* in Kansas produced two clutches of eggs in the same season; first clutches averaged 4.7 eggs, second clutches 3.5 (Legler 1960b). 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.

Clutch sizes in turtles are correlated with the size of the female (Cagle 1944b, 1950; Einem 1956; Legler 1960b; Tinkle 1961; Moll and Legler 1971). 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 carapace length and clutch size in the three females containing oviducal eggs (see below).

Reproductive 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, resulting in enlarged follicles that may not be ovulated until the following season, and in which more than one clutch per year may be produced. These phenomena are known to occur in *T. carolina* and *T. ornata* (Altland 1951; Legler 1960b), and in *T. coahuila*. Tinkle (1961) states that "counts of follicles, lutea, and eggs will give an estimate of the maximum egg production . . . but the actual production may be much lower." The maximum annual reproductive capacity of *T. coahuila* can amount to 11 eggs (maximum of 4 eggs in the first two clutches and 3 eggs (see below).

Several difficulties in using this method for *T. coahuila* were apparent: (1) that all the females collected in April had developed a full complement of potential ovulatory follicles could not be determined accurately; (2) the probable rapid disappearance of corpora lutea made it impossible to determine whether some postreproductive females had already ovulated, and, if so, how many eggs they had laid; and (3) some

postreproductive females lacked enlarged follicles, possibly because they were preserved before a new ovarian cycle had become advanced.

In April the prereproductive potential, as estimated by counts of follicles greater than 5 mm in diameter in nine mature females, was 3.9 eggs/female. As *T. coahuila* can produce more than one clutch of eggs per season, forming new follicles in each of three possible reproductive periods, the above may be an inaccurate estimate for a single year. 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. Of the July-August sample, 53% would be expected to produce two clutches. In the estimated 35% of females producing three clutches per season, the expected mean annual reproductive potential, determined by adding the mean number of eggs in each clutch, is 6.8.

As is true for clutch size, reproductive potential of *Sternotherus odoratus* varies geographically (Tinkle 1961). After comparing *Terrapene n. nelsoni* from western México with *T. o. ornata* and *T. c. carolina* 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." The mean reproductive potential (6.8 eggs/female per season) realized by an estimated one-third of *T. coahuila* females is below the potential of 8.2 (mean first and second clutch sizes added) realized by a similar portion of the *T. o. ornata* population in Kansas (Legler 1960b), but is higher than the mean single clutch size (=mean reproductive potential) of 4.2 eggs/female per season in northern *T. c. carolina* (Allard 1935).

EGG-LAYING SEASON.—The earliest date of laying indicated by preserved specimens of *T. coahuila* was approximately 3 July (corpora lutea), the latest date approximately 26 August (oviducal eggs). Legler (1960b) and Gibbons (1968c) noted that *T. o. ornata* and *Chrysemys picta*, respectively, normally retained eggs in the oviducts for 2 to 3 weeks before laying. Although length of egg retention in *T. coahuila* is unknown, if 3 weeks is added to the approximate earliest date of ovulation (early April), oviposition could 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. One female had two preovulatory follicles on 24 August, extending oviposition to the latter portion of September if ovulation were to have occurred in early September.

Incubation periods of turtle eggs are subject to wide variation depending largely upon environmental temperatures. Allard (1949) found that eggs of *T. carolina* hatched in 52 days at summer laboratory temperatures, 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 of *T. c. carolina* varied from 69 to 103 days at Washington, D.C. (Ewing 1933). Conant (1951) reported an incubation period of a single clutch of *T. c. carolina* in Ohio to be 105 days. Ewing (1933) and Allard (1948) reported hatching of *T. carolina* in September and early October. A typical incubation period for *T. o. ornata* eggs in eastern Kansas under natural conditions was about 65 days; eggs laid in mid-June usually hatch in mid-August, but may be delayed until October in years when summer temperatures are cooler than normal (Legler 1960b). Legler (1960b) 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; at 27.8°C, 70 days; and at 23.9°C, 125 days. Moll and Legler (1971) determined the mean incubation period of *Pseudemys scripta* eggs in Panama at seasonal environmental temperatures (21° to 32°C) to be 78 days.

Climatological data indicate that mean monthly air temperatures in the 7-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 Arias 1942). Mean temperatures during this period in 1965 ranged from 18.5° in November to 29.5° in July (Modesto de la Garza P., pers. comm.). If the incubation periods given by Legler (1960b), Moll and Legler (1971), and others, are assumed to approximate those of *T. coahuila* in the period from May through November when environmental temperatures would generally correspond to temperatures given for an incubation period of approximately 70 days, projected dates of hatching of the eggs contained in the three gravid female *T. coahuila* would be approximately mid-September, early October, and late October or early November.

Hatchlings appearing in October or early November from eggs laid in August should not experience thermal difficulty in emergence. Average maximum air temperatures in November (26.3°C) and December (20.7°C) (Contreras Arias 1942) would provide suitable conditions for activity; if, as seems probable, nests are placed in moist, soft soils of sedge tussocks, conditions may differ widely from those indicated by air temperatures alone. The relatively warm water of the marshes would mitigate environmental extremes.

A 1- to 3-month old hatchling was discovered in the study area on

TABLE 5. SIZE OF EGGS IN THREE CLUTCHES OBTAINED FROM OVIDUCTS OF FEMALE *T. coahuila*.

Date Preserved	Carapace Length of Female (mm)	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
		Mean \pm 1 SE		
		33.2 \pm 0.67	16.9 \pm 0.28	5.66 \pm 0.30

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. Extended periods of incubation (230 days) as reported by Driver (1946) for *T. c. carolina*, or overwintering in the egg by hatchling turtles (Myers 1952; Sexton 1957) would not be expected to occur in *T. coahuila*, which inhabit a warmer climate.

EGGS.—Nine 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. For the eggs' dimensions and weights see Table 5.

Lengths of *T. coahuila* eggs approximate those reported by Allard (1948) and Cahn (1937) for *T. c. carolina*, but their widths are slightly less. 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 (Carr 1952; Crooks and Smith 1958; Legler 1960b; Milstead and Tinkle 1967). Mean weight of the nine preserved eggs of *T. coahuila* (5.66 g) is less than mean weights of *T. c. carolina* eggs (8.4 g, Allard 1949; 9.24 g, Cunningham and Huene 1938) and *T. o. ornata* eggs (10.09 g, Legler 1960b).

GROWTH

Growth in turtles was reviewed by Cagle (1946) and Legler (1960b). They also extensively analyzed growth in *Pseudemys scripta* and *Terrapene ornata* respectively. I have followed Legler's terminology.

The usefulness of major growth-rings as indicators of growth and age depends upon four assumptions (Sexton 1959a): (1) a discernible increase in growth occurs each year, (2) one major growth-ring is added

TABLE 6. SIZE AND AGE OF JUVENILE *T. coahuila* AS DETERMINED FROM GROWTH-RINGS.

Specimen No.	Estimated plastron length at hatching ¹	Plastron length at first winter	Plastron length at second winter	Plastron length up to time of capture	Estimated age
ASU 8000	26.1 (July-Sept. 1966) ²	—	—	30.5 (15 Oct. 1966)	1-3 months
ASU 8001	29.0	36.3	43.6	49.0 (shell found)	> 1 year (?)
Field no. 66	? (Sept. 1963)	36.4	54.2	57.1 (15 July 1965)	1 year, 10 months
USNM 159578	? (Sept. 1963)	?	—	49.8 (20 Aug. 1965)	1 year
UU 3646	28.7 (July-Sept. 1959)	36.9	—	47.2 (18 Aug. 1960)	1 year

¹Measurements are in millimeters.²Probable dates of hatching and dates of collection are indicated in parentheses.

per year, (3) no major growth-rings are lost, and (4) a major growth-ring of any selected scute does not change in length after its formation.

It was possible to estimate growth and age only in a few small *T. coahuila*. Growth-rings are presumably obscured by wear. No turtles were found to be shedding their epidermal scutes. Nearly all subadult and adult individuals had a completely smooth carapace and plastron, or, at best, exhibited only traces of recently-formed growth-rings on the abdominal or pectoral scutes of the plastron. No other methods of aging were attempted.

Four juveniles collected in or near the study tract and one (shell only) from an unknown locality in the basin provide some data on approximate size at hatching and early growth, as 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 Legler (1960b). Sergeev's (1937) proportion was used to calculate previous plastron lengths.

Plastron lengths at hatching are estimated at 26.1, 28.7, and 29.0 mm in three juveniles (Table 6). One specimen (ASU 8000) may be 1 to 3 months old as estimated from its growth increment (17% of the plastron length at hatching) and from the probable season of hatching in the population (mid-July to December). September, holding a roughly median position in the hatching season, is a likely month of appearance for two other juveniles.

Legler (1960b) recorded only a 17.5% increment in plastron length of *T. ornata* in the year of hatching, a 68.1% increase in the first full year of growth, and decreasing each year thereafter (28.6% in the second

season, 18.1% in the third, etc.). Ernst (1971b) recorded a mean plastral increase of 111% in *Chrysemys picta* following hatching, but that figure includes growth of hatchlings that overwintered in the nest and whose growth began early the following year (called the "first season" by Ernst). As hatchling *T. coahuila* may emerge earlier from the nest and remain active longer than more northern species of *Terrapene*, growth in the season of hatching could be considerably greater. Two juveniles (ASU 8001, UU 3646) increased an estimated 25% and 28% of their original plastron lengths in the season of hatching. Three juveniles (ASU 8001, field 66, UU 3646) made calculated increases of 20%, 28%, and 49% of previous estimated plastron lengths (attained by the end of the hatching year) in their first full year of growth.

BIOTIC ASSOCIATES

Some *T. coahuila* had compact deposits of algal marl on the carapace, most commonly on the anterior or posterior edges, or both. Two individuals collected in December 1965 had algal encrustation on the five posterior marginal scutes of each side, the posterior portion of the third laterals, and all of the fourth laterals on both sides of the carapace; one had coatings on the first two marginals anteriorly. Color of these deposits on *T. coahuila* ranged from a pinkish hue to green.

In December 1965 and January 1966 samples were scraped from carapaces of five individuals from marshes in or near the study area. Six genera of blue-green algae (Cyanophyta) were identified from these samples: *Anacystis*, *Gloeothoece*, *Lyngbya*, *Oscillatoria*, *Pleurocapsa*, and *Spirulina*. Diatoms (genera unknown) occurred on two of the turtles together with blue-green genera. No green algae (Chlorophyta) were in any of the samples from turtle carapaces, but a sample of algae collected from a marsh in January 1966 contained the green algae *Spirogyra* and *Mougeotia*. A blue-green alga (*Gloeothoece*) and diatoms (*Synedra* and others) were also present in the marsh sample. A. T. Hotchkiss (pers. comm.) 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 hold-fast.

Many species of aquatic turtles support floras of epizoid green algae, mainly the genus *Basicladia* (Edgren et al. 1953; Proctor 1958; Gibbons 1968a; Moll and Legler 1971). *Basicladia*, a genus restricted mostly to turtles, was not found on any of the *T. coahuila* sampled, but a filamentous algal growth that was not identified (but which may have been

Basycladia) was on the carapace of an individual in the preserved series from near the study area. In 1956 John M. Legler first noted algal growth on *T. coahuila*. *Basycladia chelonum* and several blue-green algae, including *Pleurocapsa* sp., were identified from a specimen in the type series E. G. Marsh, Jr. collected in 1939.

One individual from 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 lateral scute. Pitting and eventual erosion of the shell in aquatic turtles could be caused by certain algae or fungi penetrating under the epidermal laminae (Hunt 1957, 1958). Potter (1887) described the penetration of wedge-shaped masses of the green alga *Dermaphryton radicans* into the carapace of *Clemmys* (= *Mauremys*) *caspica* of Europe. Jackson (1964, 1969) noted carapace erosion in *Sternotherus m. minor* from Florida, and suggested injuries from intraspecific aggression as a possible cause. Carpenter (1956) recorded carapace pits in *T. carolina triunguis* in Oklahoma and speculated that parasitic fungi, among other factors, might have caused the shell erosion.

Seven of 169 (4%) *T. coahuila* in the field harbored 1 to 4 small unidentified 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 when quiescent, and did not appear to discomfort the turtles; they were easily detached.

Of 48 dissected *T. coahuila*, 46% contained from 1 to 5 small, unidentified nematode worms in the stomach, some of which were imbedded in the lining. A total of 68 nematodes was in 22 stomachs, and averaged 2.4% of the volume of material in stomachs possessing them. Nematodes were in 42% of the intestines examined; one individual contained 104 and another 41. Nematodes in the latter turtle were matted together in two compact aggregations. Esch and Gibbons (1967) studied nematode parasitism in *Chrysemys picta*, reporting infection rates of 31 to 78% in mature individuals. Sex and age of the host, water temperature, and season of the year influenced the rate of infection.

INJURIES AND PREDATION

Injuries were noted in 24 of 218 (11%) *T. coahuila* examined in the field and in the laboratory. Of these 7 (3%) were burn scars, 6 (3%) were limb amputations, and 6 (3%) were scars on the shell.

Grass burning is practiced in the basin of Cuatro Ciénegas. M. A. Nickerson (pers. comm.) reported considerable burning in the basin in late March and early April 1969. On 28 March three small 100–400 m² areas that were charred black by recent burning were noted, one of which was at the *T. coahuila* study area (see "Mortality and Replace-

ment"); on 2 April a small fire was burning near the study area, and Nickerson saw a large fire, estimated to have burned "many thousands of square meters," in the east-central region of the basin.

Burn scars on the carapace of *T. coahuila* usually covered between one-fourth and one-half of the surface and consisted of rough-textured, regenerated epidermis, recently-exposed underlying bone, or raised patches of dead bone sloughing from an old wound. Legler (1960b) described worn patches of enamel-like, shiny bone during shell regeneration in burned *T. ornata*. Similar areas of exposed bone were on five of seven burned specimens of *T. coahuila*. The worst burn injury recorded was in a subadult male (ASU 5854) collected in July 1965 near the study area. All epidermal scutes of the carapace had been burned away, and the exposed bone was smooth, polished, and lacking noticeable sutures. The epidermis of most of the marginal scutes was loose and peeling away. Despite its injury the turtle appeared healthy, and its stomach contained food.

Amputations and some carapace scars probably result from attacks by predators. Four of five adults had one hind limb missing, and the other lacked its right foreleg. A post-hatchling (ASU 8000) 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 may have been inflicted by some large predator. One male had a 4-cm gash on the second left lateral scute, and several small pock-like scars, possibly tooth marks, on the carapace and plastron. In addition, the right hind leg was missing. The coyote, *Canis latrans*, could inflict wounds of this nature and possibly succeed in preying on some turtles. They are not common diurnally in the region. Only one was seen crossing the study area during the summer of 1965. Minckley (1966) described a coyote catching a large *Pseudemys scripta taylori* in a shallow lake (Laguna Grande) in the Cuatro Ciénegas basin, and found a live *T. coahuila* that was thought to have been attacked and chewed at the same locality.

Coahuilan box turtles are extremely alert while foraging and, in addition to protective coloration, seem to rely considerably on rapid movement and escape for survival. Disturbing a foraging turtle usually made it stop and raise its head, and it then remained motionless for several minutes. Another movement by the intruder usually made the turtle withdraw its head and limbs into the shell and remain motionless. Not infrequently a turtle moved away rapidly and burrowed into the mud. Some escaping individuals thrust themselves so vigorously into the mud that the rear of the shell and hind legs tilted upward at an angle.

When *T. coahuila* were handled in the field, 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 (1960b) have noted that some *T. c. carolina* and *T. o. ornata* struggle to escape while handled, whereas others close their shells and remain passive.

THERMAL RELATIONSHIPS

Cloacal temperatures of *T. coahuila* captured in the field were recorded with a Schultheis quick-recording mercury thermometer graduated in 0.2°C divisions. Even after several minutes of handling, cloacal temperatures did not change noticeably and so were not apparently affected by conduction of heat from my hand to the animal's body. Fitch (1956) noted this in recording body temperatures of small amphibians and reptiles.

Environmental temperatures recorded were: (1) water temperature at a depth of 1 to 2 cm at the site of capture (measured immediately after obtaining the cloacal temperature); (2) 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, when applicable, (3) mud substrate temperature beneath the water at the capture location.

Terminology follows Cowles and Bogert (1944) and Brattstrom (1965) for the voluntary minimum and maximum, normal activity range, and preferred or optimum temperature. The optimum body temperature is, in practice, the mean body temperature within the normal activity range; the voluntary minimum and maximum are, in practice, the lowest and highest body temperatures, respectively, recorded for free, active animals (Brattstrom 1965).

In the field 254 cloacal temperatures were secured. Almost 90% were accompanied by a simultaneous reading from the water in which a turtle was found. The remaining temperatures were from animals in terrestrial situations, such as on dirt roads or dry ground at the edge of marshes. During July and August 1965 air temperatures were recorded only for turtles captured on land, and were seldom obtained with turtles found in water. Air temperatures were recorded regularly in December 1965, January 1966, and April 1966.

ACTIVITY TEMPERATURE.—Two hundred cloacal temperatures and corresponding water temperatures were recorded. A highly significant regression ($P < 0.01$) exists between a turtle's cloacal temperature and

that of the water in which it was active. Brattstrom (1965) and Edgren and Edgren (1955) reported cloacal temperatures of *Sternotherus odoratus* closely approximating the surrounding water, and Boyer (1965) noted body temperatures of aquatic turtles in water were nearly identical to water temperatures.

Of 121 *T. coahuila* caught in marshes in July and August 1965, cloacal temperatures of 114 were 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. Only 21% of 45 turtles between 6:00 and 8:00 AM had 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. Moll and Legler (1971) reported that a basking *Pseudemys scripta* changed its antero-posterior orientation as much as 360° in one hour. In marshes almost all active *T. coahuila* were in shallow water with the carapace dry and exposed to sunlight.

During December 1965 and April 1965 and 1966, approximately two-thirds of the cloacal temperatures were higher than water temperature. Differences ranged from 0.2 to 1.3°C in December and from 0.1 to 3.4°C in April, but the mean cloacal temperature in December does not reflect this trend, being slightly less than the mean water temperature (Fig. 9). In several instances turtles that apparently had recently emerged from deep in the mud had body temperatures as much as 3.3°C 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 the surrounding water. Three emerging *T. coahuila* had cloacal temperatures 2.7°, 2.9°, and 3.0°C less than that of the surface water.

Although cool, all days during December 1965 were clear and sunny; air temperatures averaged 17.6°C. In contrast, 3 of the 4 days on which turtles were captured in January 1966 were overcast, and the air averaged 11.1°C. Some differences are to be expected, therefore, between temperature data from these two winter months. Active turtles, with carapaces exposed to air, probably are affected by low air tempera-

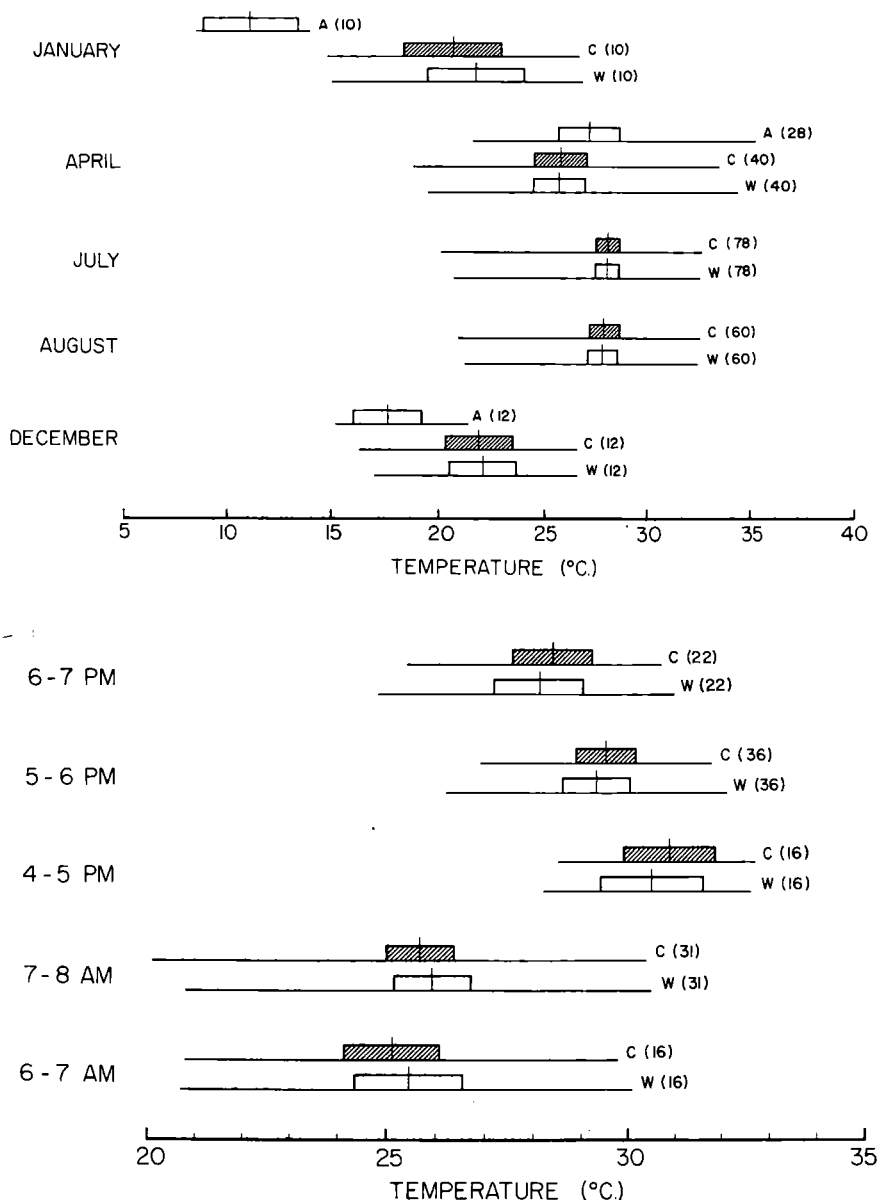


FIGURE 9.—Temperature relationships of *T. coahuila* active in marshes. Vertical and horizontal lines represent mean and range of observed variation, respectively. Blocks represent 95% confidence limits (approximately ± 2 standard errors); number of records in parentheses. Top: Seasonal variation in cloacal (C) temperatures during five months of year, showing relationship with water (W) and air (A) temperatures recorded at times of capture. Bottom: Daily fluctuation in water (W) and cloacal (C) temperatures during July and August 1965.

TABLE 7. WATER AND *T. coahuila* CLOACAL TEMPERATURES.

Month	Water		Cloaca	
	Mean \pm 1 SE	Extremes	Mean \pm 1 SE	Extremes
July (78) ¹	28.08 \pm 0.30	20.7–32.6	28.14 \pm 0.30	20.1–32.7
August (60)	27.84 \pm 0.38	21.2–32.5	27.94 \pm 0.38	20.9–32.6
December (12)	22.08 \pm 0.79	17.0–26.6	21.93 \pm 0.79	16.3–26.6
January (10)	21.75 \pm 1.12	15.0–26.9	20.67 \pm 1.12	14.8–26.7
April (40)	25.74 \pm 0.65	19.5–34.4	25.80 \pm 0.65	18.8–33.5
Hour ²				
6–7 AM (16)	25.47 \pm 0.56	20.7–30.1	25.12 \pm 0.49	20.8–29.8
7–8 AM (31)	25.93 \pm 0.40	20.8–30.5	25.68 \pm 0.36	20.1–30.4
4–5 PM (16)	30.51 \pm 0.56	28.2–32.6	30.88 \pm 0.49	28.5–32.7
5–6 PM (36)	29.33 \pm 0.37	26.2–32.1	29.53 \pm 0.33	26.9–31.8
6–7 PM (22)	28.12 \pm 0.47	24.8–31.0	28.39 \pm 0.42	25.4–30.7

¹ Number of records in parentheses.² In July and August 1965.

tures. 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 (Table 7, Fig. 9). Cloacal temperatures in December and January are significantly lower than those in April, while the April temperatures are significantly lower than records in July and August. A voluntary minimum temperature of 14.8°C (January) and a voluntary maximum of 33.5°C (April) were the extreme cloacal temperatures recorded at all seasons within marshes. These give the approximate limits of the normal activity range in shallow water. Cloacal temperature variation closely follows the seasonal changes in marsh water temperatures brought about by over-all climatic changes of the area. Mean monthly air temperatures for Cuatro Ciénegas (Contreras Arias 1942) show December and January as the coldest months, with July and August as the hottest, and with April intermediate between the two. With data presently available showing such wide seasonal fluctuations, it is doubtful that calculation of an optimum or preferred cloacal temperature would be meaningful for *T. coahuila*. Moll and Legler (1971) reached essentially the same conclusion regarding *Pseudemys scripta* in the tropics.

During July and August 1965, when most data were taken on *T. coahuila*, records were divided into 1-hour periods to test variation in cloacal temperatures at different times of day (Table 7, Fig. 9). The difference in mean cloacal temperatures between the time periods is highly significant ($F=33.2$, $P<0.01$). Cloacal and water temperatures were lowest between 6:00 and 7:00 AM, the period shortly after sunrise, before insolation raised water or cloacal temperatures. Maxima

for the time periods indicated were attained between 4:00 and 5:00 PM (Table 7). Cloacal temperatures of *Pseudemys scripta* in Panamá similarly varied with time and changing water temperatures throughout the day (Moll and Legler 1971). The few records available for midday are highest of all cloacal temperatures recorded from *T. coahuila* within marshes. The paucity of records during these intervals seems to reflect a lowered level of box turtle activity.

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 and water temperatures in morning than in the afternoon (Fig. 9) suggests more variable microclimatic conditions in marshes in the former period, and is a partial result of turtles at widely-varied stages of warming.

Ten cloacal temperatures were taken from turtles collected from pools of the Río Mesquites (Fig. 6) in July and August 1965. All were recorded in late morning or early afternoon, and temperatures of both water and cloacae were high. On 30 July, under overcast conditions, water temperatures were near 33.0°C; cloacal temperatures of five turtles ranged from 31.4 to 33.6°C.

Sinkholes (Fig. 5) are generally fed by thermal springs and have the highest water temperatures of all aquatic habitats sampled. Two in the study area ranged from 30.9°C in January 1966 to 34.7°C in October 1966 (mean of six records, 32.1°C), and from 32.8°C in January 1966 to 34.2°C in July 1966 (mean of six records, 33.5°C). Temperatures in these habitats are probably always above 30.0°C throughout the year. On 31 July 1965 a female registered 34.1°C, the highest voluntary cloacal temperature of any *T. coahuila* recorded while in water (34.0°C). Two other cloacal temperatures of turtles in posos (August 1965) were 33.4°C and 32.1°C, each 0.1° above the water temperature. Another individual seen 14 October 1966 in a sinkhole (water 34.0°C) was not caught.

T. coahuila on sedge tussocks within marshes, at the edge of a marsh, or in the grassy terrain away from water, provided an opportunity to note the effects of a thermal environment uncommon to *T. coahuila*. A female on 6 July 1965 at 6:15 AM on a dry sedge clump, had a cloacal temperature of 20.3°C (air 21.4°C); her lower temperature presumably reflected the cool soil beneath her. Another female at the edge of a marsh the previous day at 6:30 AM had a cloacal temperature of 21.8°C

(air 23.5°C). A female found resting in a horse path 4 August 1965 at 6:25 AM had a cloacal temperature of 22.4°C (air 21.1°C). The morning was cloudy, cool, and damp, with a brisk easterly wind. On the afternoon of another overcast day, 12 July 1965, a turtle in grass near a marsh, shaded and on a cool substrate, had a cloacal temperature of 28.8°C (air 31.6°C). The highest cloacal temperature recorded during this study was 34.5°C in 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 suggests that *T. coahuila* does exhibit basking behavior. The most convincing data for elevation of body temperatures by basking were obtained on 21 December 1965. Air temperatures at midday varied between 17.0 and 19.1°C under a clear, sunny sky with a moderate southerly breeze. Three turtles caught on land had cloacal temperatures considerably higher than air temperatures (mean difference 10.8°C; range 6.5–14.0°C). The mean cloacal temperature for these three turtles was 29.2°C, while three other individuals in water at the same time had cloacal temperatures 5.0 to 9.0°C 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. 9). All but 2 of 6 days during April 1966 were sunny and clear, probably contributing to the mean cloacal temperature being slightly above that of the water. On the morning of 7 April 1966, three of five turtles captured had cloacal temperatures from 0.2 to 1.7°C higher than the water, 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 *T. coahuila* on a dry substrate in summer were raised at most only 2.4°C above air temperatures. On 31 July 1965 at 8:05 AM, cloacal temperature of a female on dry ground at a marsh edge was 25.3°C, 2.1° above the air temperature (23.2°C). The morning was hazy, with a slight easterly breeze. Cloacal temperatures of two turtles also found on land during the morning 2 days later were near the high prevailing air temperatures. One had a cloacal temperature of 31.9°C (air 34.3°C), and the other registered 33.3°C (air 32.9°C). These observations further indicate that *T. coahuila* are capable of achieving elevated body temperatures, even under overcast skies. Changes in body temperature of *T.*

coahuila, and levels of heating attained while basking, appear similar to those reported for other aquatic species (Cagle 1946; Boyer 1965; Brattstrom 1965; Sexton 1959b; Moll and Legler 1971).

DAILY AND SEASONAL ACTIVITY.—In summer, *T. coahuila* were active from shortly after sunrise (about 6:00 AM) until several hours after dark (10:00 PM). 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 three marshes. Between 6:00 and 7:00 AM, air temperatures averaged 21.7°C (range 16.7–25.6°C, 34 records). Maxima 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 midday or early afternoon. Few box turtles were active in this period.

Legler (1960b) noted that most *T. ornata* in Kansas remained inactive at midday on hot summer days, and Penn and Pottharst (1940) observed midday inactivity in summer for *T. carolina major* in Louisiana. Two *T. coahuila* on 11 July 1965 at 12:15 PM were found under the thick cover of a composite shrub and sedges, at the edge of a marsh. Air temperature was 34.4°C, and cloacal temperatures of the turtles were 29.1 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 in this place at 5:00 PM had a cloacal temperature of 29.2°C, water 28.9°C.

A crude experiment was performed in the field using an adult female *T. coahuila* to determine the approximate upper limit of temperature tolerance. The turtle was tethered on a string under direct sunlight. 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; after 22 minutes at 37.5°C it made almost no attempt to close the shell. Gasping and frothing at the mouth appeared early in the experiment. Distress was evident after 7 minutes, when the body had reached approximately 35.0°C. This may approximate the maximum temperature *T. coahuila* tolerates in nature. A similar upper limit was reported for *T. o. ornata*; 37.4°C (mean of 17 records) represented the cloacal temperature when salivation (frothing) began (Riedesel et al. 1971). 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, Vinegar, and Kosh (1966) report CTMs ranging from 42.5 to 43.0°C in *T.*

carolina, and give a mean CTM of 41.6°C for several species of semi-aquatic emydids.

Water temperatures during summer at midday may often be 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. The day was clear and hot, despite a brisk easterly wind. Air temperature was 35.0°C. Water temperatures were 37.8°C in marsh 6 and 35.3°C in marsh 2-A. On 14 October 1966 at 1:15 PM open water in marsh 8 reached a temperature of 38.8°C. Such maxima are probably 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°C 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 sunny days, *T. coahuila* seem to alternate periods of activity with longer periods of rest. One male remained in uninterrupted quiescence for nearly 4 days. I recorded the turtle at 7:45 AM on 20 July 1965 and watched it dig into the base of a sedge clump. The tussock was checked each morning and evening of the following days to verify the turtle's presence. It remained there, well covered by vegetation and in shallow water, until the night of 23 July or the early morning of 24 July. Resting for several days and then resuming activity was a conspicuous feature of *T. c. carolina* behavior (Stickel 1950). Legler (1960b) noted that some *T. o. ornata* were steadily quiet for several consecutive days in summer.

Unlike other box turtles, *T. coahuila* is to some extent nocturnal, although Webb et al. (1963) observed that *T. coahuila* in captivity were inactive after dark. Marshes in the study area were visited on three nights in the summer of 1965, and on two occasions (5 and 18 July) four active box turtles were found between 8:50 and 10:00 PM. Their activity was seemingly identical to that during the day; cloacal temperatures ranged from 23.5 to 27.4°C. No turtles were sighted between 11:30 PM and midnight on 3 August 1965. Breder (1927), Allard (1935), Cahn (1937), and Stickel (1950) noted no nocturnal activity in *T. c. carolina*, and Legler (1960b) showed by the use of thread trails that the activity of *T. o. ornata* ended at dusk.

Winter activities of *T. coahuila* may be curtailed by low water temperatures, except in thermal waters. On 28 December 1964 at Posos de la Becerra, then a series of large marsh pools 13 km SW of Cuatro Ciénegas, seven *T. coahuila* were found in shallow (20 cm) water. 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 appeared lethargic when captured, most being partly buried in the flocculent bottom material. Body temperatures ranged from 7.2 to 12.4°C, mean 10.0°C. During December 1965 and January 1966 I caught no *T. coahuila* with a body temperature lower than 14.8°C.

A rudimentary laboratory experiment using adult *T. coahuila* of both sexes was performed 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. At the first successful forward movement, cloacal temperatures 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° (mode 12.0°C, mean 12.2°C). These data indicate the possible minimum effective temperature for movement in *T. coahuila* as around 12.0°C. The minimum temperature tolerated voluntarily may be 14.0 to 15.0°C. Cagle (1946) estimated the minimum effective temperature for activity in *Pseudemys scripta* to be about 10°C. Ernst (1967) found several pairs of *Clemmys guttata* copulating in 8.5°C water in Pennsylvania; cloacal temperatures of the turtles ranged from 8.0 to 10.1°C.

Diurnal activity follows ambient water temperatures more closely than air temperatures. 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 Arias (1942) gives average minimum air temperatures of 9.0, 7.6, and 9.9°C and extreme minima of -2.0, -0.3, and -1.0°C, respectively, for these months. Such low air temperatures could conceivably drive surface water temperatures below that voluntarily tolerated by *T. coahuila*, forcing them into the mud bottom of marshes where temperatures would most likely be higher. Many turtles may undergo temporary states of inactivity at night as a result of the cold, especially from December through February.

FOOD AND FEEDING

FORAGING BEHAVIOR.—Practically all turtles captured were active. Inactive turtles were found infrequently, usually concealed under a sedge tussock, beneath mats of stonewort, or in the soft mud marsh bottom.

Two marshes provided suitable places for studying foraging turtles. The south and west edges of marsh 11 were relatively open, having areas of shallow water with scattered *Eleocharis* closely cropped by horses. A



FIGURE 10.—Female *T. coahuila* foraging in a marsh near the study area, 24 August 1965. Nine mosquitofish, *Gambusia marshi*, are swimming near the turtle.

second marsh was essentially open and shallow with beds of *Chara* and grazed *Eleocharis* around the perimeter, offering an unusually good situation where turtles could be watched easily with binoculars. Feeding turtles could sometimes be approached to within a meter.

Water depth generally varied between 2 and 6 cm so that much of the turtle's carapace remained above water level and was dry. The animal nearly always held its head below the water surface as it moved forward, apparently scanning underwater. Forelimbs were frequently used to move *Chara* and basal portions of *Eleocharis* to the side while the head entered the cleared area or the turtle nipped at portions of up-rooted plant material or exposed aquatic animals. Typically the turtle occasionally raised its head out of the water, neck extended, as if surveying its surroundings (Fig. 10). These pauses usually lasted only a few seconds, but might be longer if an intruder was suspected.

The Bog Turtle, *Clemmys muhlenbergi*, in northeastern U.S., inhabits *Sphagnum* moss—*Carex* sedge marshes similar in life form to the *Chara*-*Eleocharis* marsh habitat of *T. coahuila*. Intersecting rivulets in the moss provide runways for *C. muhlenbergi* (Barton and Price 1955).

Sexton (1959b) described foraging of *Chrysemys picta* on pond surface vegetation mats in which their carapaces remained above the water and their heads extended forward beneath the water. Patterns of foraging of these two species are notably like those of *T. coahuila*, which appears, on this basis, to be as well-adapted as do these, and possibly other, aquatic emydids.

On 22 December 1965 at 2:35 PM, 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 was 23.1°C, water was 22.7°, and air 21.4°C.

Between 21 and 29 July 1965 I made 10 observations of foraging turtles; 4 were between 6:30 and 7:30 AM and 6 between 4:45 and 7:25 PM on different days. Morning and evening foraging patterns did not seem to differ. Cloacal temperatures varied between 26.3° and 32.3°C.

A female 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 she climbed partly out of water, pulling apart plant material and muddy debris with her forefeet, biting at sedge stalks thus exposed. For approximately 20 minutes this individual foraged in an area of only 25–30 cm on a side. Another individual moved approximately 3 meters in 45 minutes while foraging among clumps of *Eleocharis*. A male climbed partly 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 for periods up to a minute, largely motionless. One individual snapped and tugged on plant material with such force that the body jerked with each effort to pull the material free. Frequent turns while following narrow channels through the vegetation, use of the forelegs to expose places for feeding, and occasional pauses to survey the surroundings typified all observations of foraging *T. coahuila*.

DIET.—Literature references to the food of *T. coahuila* are few. Williams (1960) noted that captives ate dead or live sunfish and roaches. Webb et al. (1963) stated that *T. coahuila* are omnivorous and scavengers on the basis of a wide variety of foods consumed by captives.

Food items were identified to order and family, and, where possible, to genus and species. Plant material was lumped into a single category for volume determination. 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): (1) percentage of stomachs in which each kind of food occurred (frequency of occurrence); (2) mean of the

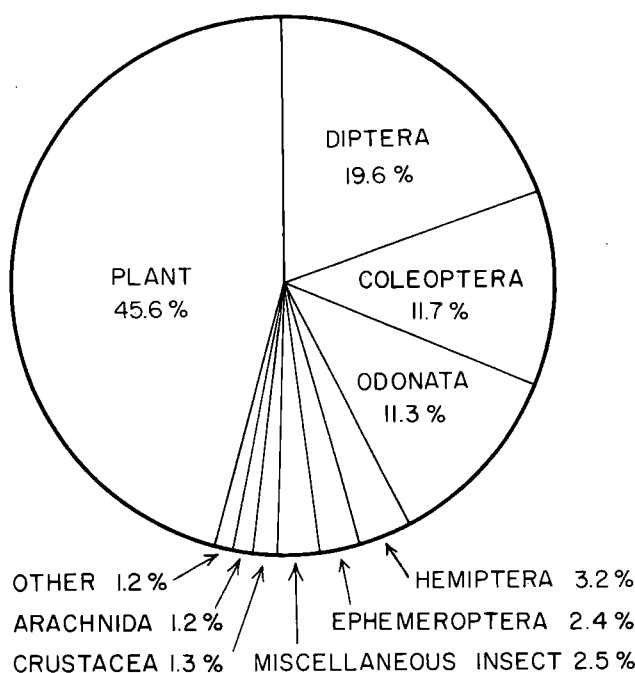


FIGURE 11.—Composition of diet by percentage of total volume of food in stomachs of 45 *T. coahuila*.

percentage of volume comprised by each of the kinds of food in stomachs containing the food (individual volume); and (3) percentage of the total volume represented by each kind of food.

Three stomachs were empty and calculations presented in Table 8 and shown graphically in Fig. 11 are based on 45 stomachs 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 most appeared considerably greater than stomachs.

Based on percentage of total volume, insects (50.7%) and plant material (45.6%) are by far the most prominent components of the diet (Fig. 11). Crustaceans (1.3%), spiders (1.2%), and fishes (0.5%) are relatively much less frequent. Plant material was found in 84.4% of the stomachs and consisted of the following kinds with the frequency of occurrence of each: *Eleocharis rostellata* 64.4%, mushroom 15.6%, *Chara* spp. 11.1%, and large unidentified seeds 6.7%.

Several groups of insects are prominent in the diet. Of the 29 insect families identified (Table 8) 19 have one or more aquatic stages in

TABLE 8. QUALITATIVE AND QUANTITATIVE ANALYSIS OF FOOD UTILIZED BY *T. coahuila*.

Taxon	Stomach (n=45)			Intestine (n=48)
	Frequency of Occurrence	Mean % Individual Volume	% Total Volume	Number in which found
Plant material	84.4	—	45.61	48
Ephemeroptera				
Baetidae (n.) ¹	20.0	9.0 (1-24)	2.31	0
unidentified (n. & a.)	4.4	2.2 (2-3)	0.04	2
Odonata				
Aeshnidae (n.)	2.2	13.1	0.27	0
Agriionidae (n.)	24.4	8.1 (2-23)	1.84	14
Gomphidae (n.)	4.4	27.3 (20-35)	1.09	4
Libellulidae (n.)	26.7	30.1 (tr.-96)	7.14	10
unidentified (n.)	2.2	24.5	0.94	2
Orthoptera				
Acrididae (n. & a.)	4.4	13.3 (12-14)	1.07	1
Hemiptera				
Belostomatidae (a.)	2.2	23.9	0.56	3
Nabidae (a.)	2.2	4.5	0.05	0
Naucoridae (n. & a.)	24.4	10.5 (1-41)	2.03	30
Nepidae (a.)	0	—	—	2
Notonectidae (a.)	0	—	—	1
Pentatomidae (a.)	2.2	31.7	0.48	1
Podopidae (a.)	0	—	—	2
Veliidae (a.)	4.4	0.9	0.05	2
unidentified (n. & a.)	8.9	0.7	0.04	5
Coleoptera				
Curculionidae (a.)	24.4	25.2 (tr.-98)	8.98	22
Chrysomelidae (l.)	0	—	—	1
Dytiscidae (l.)	4.4	23.9 (4-44)	0.44	5
Dytiscidae (a.)	6.7	1.9 (tr.-5)	0.04	1
Hydrophilidae (a.)	11.1	6.9 (1-25)	1.57	8
Limnebiidae (a.)	4.4	2.9	0.06	0
Oedemeridae (a.)	4.4	6.5 (4-9)	0.17	0
Staphylinidae (a.)	2.2	0.5	0.02	0
Tenebrionidae (a.)	2.2	3.3	0.12	0
unidentified (a.)	2.2	9.1	0.27	8
Trichoptera				
Hydroptilidae (l.)	4.4	0.9	0.07	0
Lepidoptera				
Microlepidoptera (a.)	2.2	0.9	—	0
unidentified (l.)	2.2	14.3	—	1
Diptera				
Chironomidae (l.)	6.6	0.7	0.04	0
Culicidae				
Chaoborinae (l.)	15.6	0.9 (tr.-2)	0.14	0
Culicinae (l.)	2.2	0.3	tr.	0
Culicidae (p.)	6.7	0.9	0.06	0
Ephydriidae (p.)	0	—	—	1
Stratiomyidae (l.)	64.4	29.9 (3-99)	18.59	39
Stratiomyidae (p.)	2.2	6.3	0.24	0
Tipulidae (l.)	6.7	8.8 (2-18)	0.46	0
unidentified (all stages)	6.7	0.4	0.04	2

TABLE 8.—Continued

Taxon	Stomach (n=45)			Intestine (n=48)
	Frequency of Occurrence	Mean % Individual Volume	% Total Volume	Number in which found
Hymenoptera				
Apoidea (a.)	2.2	1.2	0.07	1
Formicidae (a.)	8.9	7.6 (1-28)	0.53	13
unidentified Insecta (all stages)	11.1	3.6 (tr.-11)	0.50	9
Arachnida				
Araneae-Argiopoidea	8.9	14.9 (1-44)	1.21	0
Crustacea				
Amphipoda				
Talitridae				
<i>Hyalella azteca</i>	17.8	5.5 (tr.-36)	0.45	3
Isopoda				
Armadillidiidae				
<i>Armadillidium vulgare</i>	4.4	16.9 (14-20)	0.46	4
Cirolanidae				
<i>Sphaerolana interstitialis</i>	2.2	35.7	0.24	1
Ostracoda				
Cypridae	22.5	0.9 (tr.-2)	0.14	13
Mollusca				
Gastropoda				
Hydrobiidae				
<i>Durangonella</i> sp. & <i>Paludiscala</i> sp.	15.6	0.4 (tr.-2)	0.04	9
Osteichthyes				
Cyprinodontiformes				
Cyprinodontidae				
<i>Cyprinodon atrorus</i>	2.2	47.4	0.22	1
Poeciliidae				
<i>Gambusia marshi</i>	2.2	5.5	0.31	0
Serpentes				
Colubridae				
<i>Natrix erythrogaster</i>	0	—	—	1

¹ Insect stages abbreviated: n., nymph; l., larva; p., pupa; a., adult.

their life cycles. Stratiomyid fly larvae were the most frequent animal food in the diet, occurring in nearly two-thirds of all stomachs containing food, and were important on a volume basis (nearly one-fifth of total volume). Many stratiomyid species live in shallow stagnant pools or in mud. Adult curculionid beetles were in almost one-fourth of stomachs and were an important component by volume. Although the adults

are not truly aquatic, the larvae of some of these beetles live in the stems or roots of aquatic plants. Libellulid dragonfly and agrionid damselfly nymphs were present in more than one-fourth of the stomachs. Odonata adults are seen frequently in and around marshes in the study area. Naucorid nymphs and adults made up the bulk of the hemipterans recorded. These bugs may be easier for box turtles to catch, as they move more slowly through submerged vegetation than other groups of aquatic hemipterans occasionally eaten. Baetid mayfly nymphs occurred in one-fifth of the stomachs.

Most of the insects *T. coahuila* ate were presumably obtained from the water, with the exception of curculionid beetles and other terrestrial forms encountered rarely during overland movements or possibly after having fallen into the water from overhanging vegetation.

A total of 167 amphipods was found in 8 turtles, giving a mean of 20.9 amphipods for those stomachs in which they occurred. The mean is strikingly high because of a single individual foraging in a low bed of *Chara* on the bottom of a poso (Fig. 5) in water about 25 cm deep; its stomach contained several small fragments of *Chara* along with 141 amphipods, 1 cirolanid isopod (*Sphaerolana interstitialis* [Cole and Minckley 1970]), and remains of ostracods and small snails. Tiny amphipods, *Hyalella azteca*, may represent a primary food item the turtle was hunting in the *Chara* beds, but amphipods made up less than 0.5% of the total volume for all food items. On 4 April 1966 amphipods occurred in 6 stomachs of 17 *T. coahuila* collected from marshes, but the number in any one stomach did not exceed 14, mean 4.2. Amphipods were plentiful during April in the marshes and clung to the skin of box turtles when they were removed from the water.

Of five box turtles collected on dirt roads adjacent to marshes, three had food in their stomachs. 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 individual volume, and the only recorded rove beetle (Staphylinidae). The third contained 39 small ants, 19 tiny limnebiid beetles, a grasshopper nymph, and a terrestrial isopod, *Armadillidium vulgare*. The turtles probably ate these items while traveling overland between marshes.

T. coahuila can apparently discriminate small objects, as indicated by the abundance of such items as amphipods, mayfly nymphs, veliid bugs, chaoborin midge larvae, ostracods, and ants. These groups, although they occurred with a frequency comparable with the other taxa listed, were not important items on a total volume basis. Average numbers of mayfly nymphs, ants, and limnebiid beetles indicate that they

were significant to certain individuals, but, when compared by this method these items assume a greater apparent importance in the overall diet than is actually the case. Cyprinodontid fishes, cirolanid 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 singularly important only to a few individuals in which a single item frequently comprised a large percentage of the individual volume in stomachs otherwise nearly lacking any other food.

Little can be said regarding seasonal fluctuations in food habits of *T. coahuila* because turtles were collected only in late summer and spring. Frequency of occurrence, combined with the mean of the individual volume percentages for the July-August sample vs. the April sample show the relative prominence of the various foods in the diet. Curculionid and hydrophilid beetles were present in far greater numbers in turtles taken in summer than in spring specimens. Ants were absent in individuals taken in spring, but caddisfly larvae and midge larvae appeared more frequently in the spring sample. Stratiomyid larvae occurred in more spring than in summer specimens, but made up less of the stomach volume in spring.

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. Barton and Price (1955) similarly found a large number of *Carex* seeds in 11 *Clemmys muhlenbergi* they examined from Pennsylvania.

Five individuals were collected in large, relatively deep (15-30 cm) pools near Río Mesquites (Fig. 6). Of these, three had eaten one fish each: two *Cyprinodon atrorus* and one *Gambusia marshi*. These were the only fish found in the entire sample of 48 turtles. These and other fish species were abundant in river pools where foraging box turtles were often seen. In December 1964 at Posos de la Becerra, Walter K. Taylor saw a male on land feeding on a dead cichlid fish, *Cichlasoma* sp. Although Williams (1960) watched a captive *T. coahuila* capture a live fish in shallow water, most fishes the turtles eat probably are dead or dying. Only two regularly visited marshes contained fishes: *Gambusia marshi* and *G. longispinis* in marsh 11; and *G. marshi*, *G. longispinis*, *Cyprinodon bifasciatus*, and *Cichlasoma* spp. in marsh N-3. Two turtles from marsh 11 preserved in July 1965 contained no trace of fishes.

On several occasions *T. coahuila* were observed foraging in pools along the river and in marshes while many small fishes (*Gambusia* and *Cyprinodon*) swam nearby, seemingly within their reach, but the turtles

ignored them. My field notes on a turtle foraging in shallow water on 24 August 1965 are typical: "*Gambusia marshi* swam to within 2 cm of the animal's head, circling the turtle, and apparently searching for bits of food material exposed in the mud stirred up by its activity. The turtle paid no attention to the fish." *T. coahuila* were never seen chasing fishes.

Remains of a juvenile water snake, *Natrix erythrogaster*, were in the intestine of a female *T. coahuila* collected in August 1965. Aside from fishes, this was the only record of predation on a vertebrate. The snake seemed fresh and was probably eaten alive or right after having been killed. None of the other reptiles and amphibians observed in the marshes were present in any *T. coahuila* examined. *T. ornata* and *T. carolina* sometimes feed on vertebrates, chiefly amphibians, lizards, and snakes (Babcock 1919, Eaton 1947, Norris and Zweifel 1950, Merhtens and Hermann 1951, Klimstra and Newsome 1960, Hutchison and Vinegar 1963).

Of four species of emydid aquatic turtles Lagler (1943) examined in Michigan, *Emydoidea blandingi* and *Chrysemys picta* showed food preferences similar to *T. coahuila* in that the insects eaten were primarily aquatic, immature stages of dragonflies and damselflies, 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. picta*. *Chrysemys picta* is more similar to *T. coahuila* in its extensive utilization of various kinds of aquatic plants, which made up 61.5% by total volume, whereas plants were a relatively insignificant component (3.9%) in *E. blandingi*.

Knight and Gibbons (1968) reported that a single river population of *C. picta* in Michigan ate plants (chiefly filamentous algae) in amounts ranging from 30 to 40% of individual stomach volumes. This *C. picta* population also ate large numbers of midge larvae and cladocerans, demonstrating opportunism not unlike that shown by some *T. coahuila* in their occasional extensive consumption of amphipods or *Eleocharis* seeds. Webb (1961) recorded midge larvae, ants, caddisfly larvae, and small hemipterans in stomachs of 8 map turtles, *Graptemys pseudogeographica*, in Oklahoma, and also found a specimen "... gorged with grasshoppers" and one stomach filled with bermuda grass (*Cynodon*) and fogwort (*Lippia*). As noted earlier, *Clemmys muhlenbergi* apparently often feeds on seeds of sedges, and is also like *T. coahuila* in consuming insects, but 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

TABLE 9: MOVEMENTS OF *T. coahuila* IN THE STUDY AREA.¹

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

¹ Measurements are mean straight-line distances in meters between successive points of capture.

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

T. coahuila is opportunistic and omnivorous, feeding extensively on aquatic plants and insects. Variation in kinds and numbers of food items from one turtle to another suggests that *T. coahuila* feeds on whatever is available. The population studied more closely resembles aquatic species of other genera in its food habits than it does the terrestrial species of *Terrapene*.

MOVEMENTS

Distance between 54 successive capture sites of *T. coahuila* were measured. Field distances were recorded to the nearest meter and map distances to the nearest half meter. Table 9 shows that 76% of recorded movements were within the marsh where the animal was previously marked, and 61% of the movements were by females. The mean distance for each movement of males and females in the same marsh is not significantly different ($P > 0.30$), so movements of the sexes were combined to obtain a mean straight-line distance of 12.8 m between points of capture.

Because a maximum of four movements was recorded for only two individuals, and two movements for four individuals, the data do not permit such refined home range calculations as the center of activity, the mean recapture radius (Hayne 1949a; Tinkle and Woodard 1967), or the minimum area method (Hayne 1949a). Fitch (1958) and Legler

(1960b) both used a simpler (and perhaps more vulnerable) method 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. Using the same capture radii technique, Ernst (1970) found the home range of *Clemmys guttata* to be biased toward a size over four times greater than the minimum area home range.

Despite the evident drawbacks of assuming the home range to be circular, if 12.8 m is considered as the average home range radius of *T. coahuila*, the mean diameter is 25.6 m. One factor that obviously affects this assumption 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 ranged from 3.5 to 15.0 m, mean 8.2 m. In the two largest marshes 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 largest marshes. The data show a slight difference, but the similarity of distances moved is more impressive and indicates that *T. coahuila* in the study tract utilize areas of roughly equal size regardless of the size of the marsh.

All marshes in the main study area are oriented in a northeast-southwest direction (Fig. 4) and so it is not surprising that 20 of 39 turtle movements within marshes were either northeast or southwest, following the long axis of a marsh. Five were in the opposite directions, northwest or southeast, nine movements were recorded as directly north or south, while only five were east or west.

A fairly direct correlation exists between time separating captures and distance traveled. Time between captures in the same marsh ranged from 1 to 464 days, 61 percent of the intervals were less than 50 days, and the mean distance of movement 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.

Home range sizes have been estimated for several species of *Terrapene*. Stickel (1950) reported the average maximum diameter of the home range for *T. c. carolina* in Maryland as 100.6 m for males and 112.8 m for females. The mean distance between successive points of capture was 118.9 m for *T. c. carolina* in New York (Nichols 1939c). Successive capture distance of *T. c. carolina* in Indiana was 69.5 m, or an average home range diameter of 139 m (Williams 1961). Williams (1961) also measured the maximum distance between any two farthest captures. The result was 114.2 m, a mean home range diameter similar to that reported by Stickel (1950). Mean distance traveled by *T. carolina triunguis* in Oklahoma between successive hibernacula in successive years

was 49.4 m, and in the same year 51.2 m (Carpenter 1957). If these distances are considered as radii, the approximate home range diameter is 100 m in the Oklahoma *T. c. triunguis* population. Distances between captures of *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 1960b.)

The estimated home range size of *T. coahuila* is considerably smaller than those of the terrestrial species of the genus that have been studied. *T. ornata*, a prairie grassland species, utilizes larger areas than *T. carolina*, a woodland species. Home range size and population density (see below) are seemingly closely correlated with habitat in the genus *Terrapene*.

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; Emlen 1969). Few (less than 15%) of a population of *Chrysemys picta* in a Michigan marsh moved farther than 100 m during one summer (Gibbons 1968c). Among a population of *Pseudemys scripta* in Panama, Moll and Legler (1971) reported mean lengths of home ranges in hatchlings, juveniles, and adults as 34, 61, and 287 m, respectively.

Foraging box turtles keep a web-like system of trails open in most Cuatro Ciénegas marshes, thus maintaining a flow of water in the small rivulets through the trails. As *T. coahuila* seldom move in a direct line, but turn randomly within the rivulet reticulum, straight-line distances between points of collection do not represent the animals' actual pattern of movement.

T. coahuila occasionally enter large sinkholes (Fig. 5), where they easily elude capture by swimming along the bottom under 20 to 50 cm of water and disappearing beneath the undercut banks. They remind one of *Sternotherus* or *Kinosternon* in their rapid, elusive swimming ability. Milstead (1967) referred to *T. coahuila* as an "awkward" swimmer, but I consider it remarkably agile.

Most *T. coahuila* tend to remain within a given marsh for relatively long periods (Table 10). Only 11 of 52 (21%) turtles in the main study area moved from one marsh to another. If direct, the animals would have crossed barren ground and most distances traveled would have been less than 100 m. They could probably cross these stretches only at times of day when temperatures would permit, as in the early morning or late evening. Some turtles may have moved to new marshes by following more indirect, connecting water courses. *T. coahuila* were

TABLE 10. DURATION OF TIME SPENT IN ONE MARSH BY *T. coahuila*.¹

Month in Which Turtle Captured for First Time	Number of New (unmarked) Turtles Captured in Month	Number Subsequently Recaptured	Number Recaptured in Same Marsh After 1 Yr.	Mean Number of Months Elapsed Between First & Last Captures
December 1964	13	9 (69%)	4	11.1 (4-19)
April 1965	11	5 (45%)	5	9.6 (4-12)
July 1965	61	20 (33%)	5	7.8 (1-12)

¹Data are from 34 turtles recaptured at least once in a later sampling period.

sometimes seen on land on overcast days. Webb et al. (1963) noted that *T. coahuila* moved overland during rainy periods.

About one-fifth of the *T. coahuila* recaptured in more than a year and a half had made intermarsh movements. This suggests that some individuals are either transients or shift their home ranges. Howard's (1960) hypothesis of innate vs. environmental dispersal could be readily tested in this species. It should also be possible to determine what environmental factors are used in orientation during intermarsh dispersal. Experiments of Gould (1957, 1959; see also Lemkau 1970) suggest that *T. carolina*, when removed from their normal home range, employ sun orientation possibly similar to the mechanism occurring in birds and anurans. But Emlen (1969) reported that land-displaced *Chrysemys picta* used visual recognition of local topographic landmarks to return to their home pond; celestial navigation was all but totally discounted over the short (100 m) experimental homing distances.

POPULATION

COMPOSITION.—Through July 1966, 164 adult *T. coahuila* of known sex were captured. Only three were juveniles, less than 2% of the sample from the study tract population. This probably reflects their cryptic coloration, small size, and possibly more secretive habits. For example I discovered one juvenile only after seeing a slight movement when it pulled its head into the mud beneath the water surface. Stickel (1950) and Legler (1960b) found many fewer juveniles than adults in populations of *T. c. carolina* in Maryland and *T. o. ornata* in Kansas.

Mean carapace length of 70 male *T. coahuila* (108.9 mm) is significantly ($P < 0.01$) larger than that of 94 females (100.9 mm) (Brown 1971). A comparison of carapace lengths of field-caught turtles with

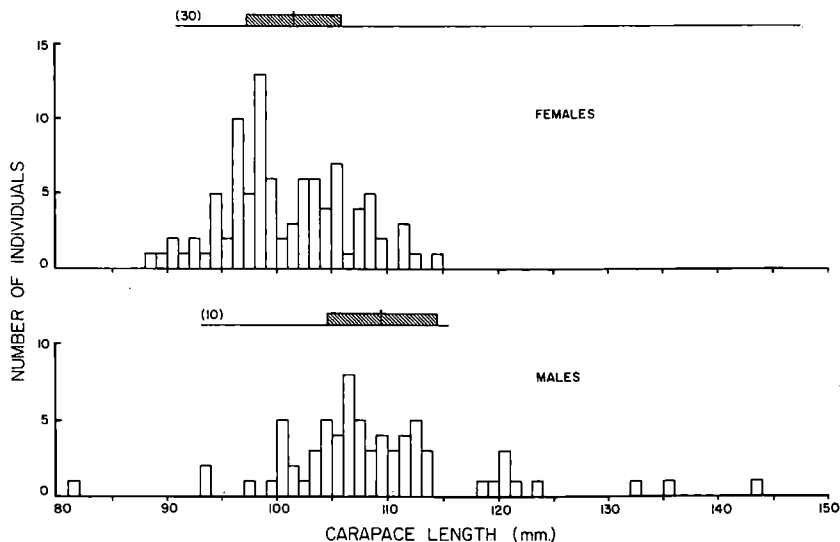


FIGURE 12.—Frequency distributions of body size in 164 *T. coahuila* (70 males, 94 females) from study area. Bar diagrams show size of sexually mature individuals examined in the laboratory. Horizontal and vertical lines represent range of observed variation and mean, respectively; blocks represent 95% confidence limits. Sample sizes in parentheses.

the size of sexually mature individuals of both sexes (Fig. 12) 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. Therefore most turtles captured were either sexually mature or approaching maturity. Modes of both sexes are within the 95% confidence ranges for size of sexual maturity (females 95–105 mm, males 105–115 mm). A majority of turtles, especially females, are clumped at the lower end of the confidence range (Fig. 12). Cagle (1954) noted a similar concentration of *Chrysemys picta* near the size of attainment of sexual maturity. Growth in *C. picta* is apparently greatly reduced at that time (Cagle 1954; Gibbons 1968b; Ernst 1971b). Legler (1960b) determined that growth in *T. o. ornata* stops about 3 years after reaching sexual maturity in both sexes, and his histogram of plastron lengths shows a close agreement with percentages of sexually mature *T. ornata*; 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, a ratio of 1.00 male to 1.34 females. The sex ratio may vary seasonally, although females did not significantly

TABLE 11. SEX RATIOS OF *T. 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
All Months Combined	70	42.7	94	57.3	1.00:1.34	3.22	>0.05

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 11).

In *T. o. ornata* Legler (1960b) reported a male/female ratio of 1.00:1.69 among 164 adults in Kansas. Nichols (1939a) reports a male/female ratio of 1.00:0.63 of 387 *T. c. carolina* from New York, but Stickel (1950) recorded a male/female ratio of 1.00:1.09 in 245 adult *T. c. carolina* from Maryland.

Gibbons (1970) reviewed sex ratios in some aquatic turtle populations. Apparent discrepancies in reports of *Chrysemys picta*, *Malaclemys terrapin*, *Pseudemys scripta*, and *Terrapene carolina* are seemingly due largely to one or more of the following factors: (1) seasonal changes in activity, as in *Malaclemys*, where Cagle (1952) points out that the large proportion of males (4.4 males/female) seemed to result from a movement of females toward shore during the nesting season; (2) a misinterpretation of the sexual difference in size when secondary sex characters appear or when the turtles become sexually mature; (3) different sampling techniques employed (Ream and Ream [1966] investigated this factor, finding significant differences between juvenile:male:female ratios of *C. picta* in four of five sampling methods tested); and (4) genetic differences between ecologically isolated conspecific populations displaying little or no interpopulation gene flow (Auffenberg and Weaver [1969], for example, reported male/female ratios of 1.00:2.08, 1.00:2.00, and 1.00:1.15 in three populations of *Gopherus berlandieri* inhabiting small, isolated hills [lomas] in extreme southern Texas).

Although the last factor may well be applicable to aquatic as well as to terrestrial species, the second factor listed above appears to have caused 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 the genera *Pseudemys*, *Chrysemys*, and *Graptemys*, in which females reach ma-

turity 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 1.00:0.76, closely approximating the 1.00:0.78 ratio for a Minnesota population of the same species reported by Ream and Ream (1966), who distinguished juveniles from adult males and females throughout their study. Gibbons (1968b) reported a male/female ratio of 1.00:0.89 for a Michigan population of *C. picta*, concluding that the slight divergence from a 1:1 ratio resulted chiefly from the method of determining maturity in females. This may well be one reason for the widely divergent results of Nichols (1939a) and Stickel (1950) on the sex ratio of *T. c. carolina*.

Most *T. coahuila* in the samples were sexually mature, so the sex ratios given (not considering juveniles) may show an actual difference in adult population structure. Female *T. coahuila* in search of nesting sites during the reproductive period may tend to travel more often and farther than males, increasing the probability of their capture. The sex ratios themselves (Table 11) offer the only evidence for seasonal differences in activity.

DENSITY.—The study tract was 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 not included in daily sampling. Although the choice to limit the study area to a given series of marshes was arbitrary, considerable expanses of unfavorable dry habitat separated marshes in the main area from outlying ones. In some instances 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 were probably affected by turtles moving between main and surrounding marshes, but the extent of dispersal was difficult to estimate. The following factors suggest that recruitment of the population by immigration, or loss of emigration, caused negligible error in the census: (1) marshes are distinct communities with sharply-defined borders, and box turtles are largely confined to them; (2) although some overland movements do occur, salt grass communities in surrounding dry, often bare, zones are effective barriers to *T. coahuila* dispersal—the main study area is fairly well set off from other marshes by these unfavorable habitats; (3) recaptures of *T. coahuila* show that they have a tendency to remain in one marsh for long periods (more than 1 year in 41% of 34 recaptured turtles, and more than 1.5 years for

two individuals); (4) population size from December 1964 through April 1966 in the main study area was relatively stable (Table 12), 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 ranges overlapped a study area boundary in continuous favorable habitat was not present in my study.

In the main study tract 114 *T. coahuila* were captured a total of 203 times; 31 (27%) were recaptured once, 9 (8%) twice, 9 (8%) three times, 2 (2%) four times, and 1 individual (1%) was recaptured five times, the maximum number of recaptures obtained. Slightly less than half (46%) of the individuals were recaptured at least once. Four turtles marked outside the main study area were subsequently recaptured in it and were counted as "new," giving 118 first-capture individuals. Two turtles marked in December 1964 and in April 1965 were found dead on 2 July 1965. Thus a total of 116 was used in all computations on census samples taken after July 1965. Estimates of numbers and density of the population apply to more than 98% adults.

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) noted that only a large influx of transients would be likely to disturb the ratio of marked to unmarked animals significantly.

A second major assumption in the sampling is that all animals in the population, both marked and unmarked, have equal chances of being collected. There is some evidence that marking had an adverse effect on *T. coahuila* behavior, causing slight deviations in recapture frequencies from those expected on the basis of random occurrence. Recapture frequencies 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 caught. Departures from the Poisson distribution indicate that any recapture class has a chance of capture greater or less than random expectation.

Four recapture classes (0 to 3 or more recaptures) showed highly significant departures from the Poisson series ($P < 0.0001$). 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 catching them. This was followed by a period of the next several days, or even weeks in some marshes, without captures. Marked box turtles apparently moved into seclusion. They could also have become more wary because of my activity during July and August 1965 when the study tract was visited daily, lowering second or third captures. In subsequent sampling periods, after monthly intervals with no human intrusion, normal activity resumed and recaptures increased. Tinkle (1958a) noted that marked *Pseudemys* and *Graptemys* in rivers were warier than unmarked turtles. Sexton (1959b) found marked *Chrysemys picta* difficult to recapture, while unmarked individuals could be approached and netted with relative ease.

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 estimates. A preliminary sample of animals is marked and released into the population, and a later sample is examined for marked animals.

Fitch (1963, 1965), working with snakes, divided the season's records into monthly intervals and then lengthened the preliminary sampling periods successively, obtaining population estimates at different points in time through a collecting season. Using the same technique I sampled the *T. coahuila* population 10 times between December 1964 and October 1966. Each sampling period was separated by intervals of 2 to 4 months, but records were treated as seven units to obtain workable sample sizes. Successively increasing the length of time of the first (or preliminary) sample periods (Table 12) 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 Lincoln index formula is: $\frac{P}{83} = \frac{70}{37}$, or $P = 157$. The pop-

ulation estimated by single census ratios ranged from 146 to 171 individuals, or a density of 53.7 to 62.9 turtles per acre (132-155/ha).

Hayne (1949b) presented a modification of the Lincoln index census. 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 propor-

tion of marked animals. Using the same census samples, 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 (135/ha).

Another mark-recapture technique used was the multiple census or Schnabel method, in which 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). As turtles were caught in the main study tract on 57 days, 57 samples were available. Prior to calculations, corrections were made for known mortality and removals. The multiple census indicated a population of 164, or 60.3 turtles per acre (149/ha). 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

TABLE 12. NUMBERS AND DENSITY OF *T. coahuila* IN MAIN STUDY AREA OF 11 MARSHES (TOTAL AREA 2.72 ACRES) FROM DECEMBER 1964 TO OCTOBER 1966 (SEE TEXT FOR DETAILS).

Method	Sampling Periods		Estimated Population Size	Population Density (Turtles/Acre)
	Preliminary	Follow-up		
Single Census: Petersen Type, or Lincoln index. Fitch's successive lengthening of sample periods	Dec. 1964	April 1965– Oct. 1966	162	59.6
	Dec. 1964– April 1965	July 1965– Oct. 1966	171	62.9
	Dec. 1964– July 1965	Aug. 1965– Oct. 1966	157	57.7
	Dec. 1964– Aug. 1965	Dec. 1965– Oct. 1966	153	56.3
	Dec. 1964– Jan. 1966	April 1966– Oct. 1966	155	57.0
	Dec. 1964– April 1966	July 1966– Oct. 1966	146	53.7
Hayne Method: increasing proportion of recaptures.	Six census samples used above.		149	54.8
Multiple Census: Schnabel Type ¹	daily (57 capture-days)		164 (135–208)	60.3 (49.6–76.5)

¹95% confidence limits in parentheses.

size, and that between 49.6 and 76.5 turtles per acre (122-189/ha) includes the actual population density in the study area. Results from the three census methods are summarized and compared in Table 12.

Considering all 11 marshes in the main study area as a unit, the total ecological (i.e., marsh habitat) range is 2.72 acres (1.102 ha). Population densities reported here for *T. coahuila* are based on this total area. The main reason for doing so is that 21% of the turtles recaptured in a sampling period after they were first marked had changed marshes. Inter-marsh dispersal might 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, or 148 per hectare) is, therefore, an average density for all marshes in the main study area. It does not take into account spatial relationships of turtles within marshes. Most turtles were caught in open places, where they were more easily seen than in dense vegetation.

Several careful population density estimates have been made for the genus *Terrapene*. Stickle (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 (1960b) estimated the average population density of *T. o. ornata* on 220 acres of grassland in Kansas to be 1.3 turtles per acre; densities were higher, 2.6 to 6.3 turtles per acre, in the most favorable pasture habitats.

Population studies of aquatic turtles have often compared relative abundance of different species from various habitats where obtaining reliable estimates of numbers is difficult (Cagle and Chaney 1950; Tinkle 1958a, 1959b). Other studies have provided data on population densities in natural populations. Cagle (1942) estimated numbers of *Chrysemys picta* and *Pseudemys scripta* in two small stock ponds in Illinois. Densities calculated from his data are 142 and 556 *C. picta* per acre, and 72 and 206 *P. scripta* per acre. Moll and Legler (1971) report a density of 77 juvenile and young adult *P. scripta* per acre in a Panama lagoon. Pearse (1923) reported a density of 5 *C. 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 Ream and Ream (1966) estimated in the same bay, calculated density is 1.6 turtles per acre. Sexton (1959b) reported densities varying between 40 and 166 *C. picta* per acre (depending on surface levels) in five Michigan ponds. Gibbons (1968b) and Ernst (1971c) provide density figures of 233 and 239 *C.*

picta per acre in open water of Michigan and Pennsylvania marshes, respectively.

Probably 60 turtles per acre (148/ha) is representative of *T. coahuila* population densities in most small marshes in the Cuatro Ciénegas basin, as the study area does not appear atypical. The aquatic *T. coahuila* thus occurs in densities roughly comparable to the aquatic species *Chrysemys picta* and *Pseudemys scripta*, and at considerably higher densities than its terrestrial congeners, *T. carolina* and *T. ornata*.

MORTALITY AND REPLACEMENT.—Proper analysis 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 no natural size groups that might indicate age were apparent in *T. coahuila*.

Few mortality rates in any phase of the life cycle of turtle populations have been published. Probable reasons for the lack of information are the comparatively low year-to-year mortality of adult turtles and their relatively long life spans, making it difficult to follow a population for the many years that would be necessary to measure age-specific mortality.

Prenatal mortality may take the greatest toll in many turtle populations. Moll and Legler (1971) reported that predators, chiefly lizards (*Ameiva*) and armadillos (*Dasypus*), robbed 213 of 231 nests of *Pseudemys scripta* in Panama. Predators destroyed many nests of *Gopherus berlandieri* in southern Texas (Auffenberg and Weaver 1969). Only an estimated 2 percent of an annual complement of 6,000 *Chrysemys picta* eggs in Michigan survived to become part of the population (Gibbons 1968b); egg predation was thought to be a major factor. Mortality curves (Slobodkin 1961) of the *C. picta* population seemed to fit two general patterns: type IV, heavy mortality in the young (i.e., egg) stages; and type III, constant mortality rate with age in the mature segment of the *C. picta* population (Gibbons 1968b). Mortality affecting immature *C. picta* (which comprised an estimated 60 percent of the population) was judged to be constant but lower than that affecting adults, but Gibbons seemingly did not account for greatly reduced growth rates after maturity. This appears to have had nearly as great, if not greater an effect on the survivorship data than did the supposed greater exposure to environmental hazards with increased activity associated with reproduction in mature turtles as Gibbons (1968b) suggested.

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. Several *T. coahuila* had serious carapacial burn scars, and some mortality can probably be attributed to fires. Several small patches of recent burning were noted in spring 1969 by M. A. Nickerson (pers. comm.), one of them within the study area. Two dead marked *T. coahuila* Nickerson found had burn scars, circumstantial evidence that fire killed them.

The population of *T. coahuila* studied was composed of approximately 57% adult females. Assuming that all were sexually mature, probably 90 females were capable of reproduction in the adult population of around 160 individuals. The annual egg production of these females may be about 400 eggs per season if (1) all 90 deposit at least a single clutch averaging 2.7 eggs (240 eggs produced); (2) if 47 (53%) deposit a second clutch averaging 2.4 eggs (110 eggs produced); and (3) if 31 (35%) deposit a third clutch averaging 1.7 eggs (50 eggs produced). To maintain a stable population individuals dying each season must be replaced. If adult mortality is low, a total annual complement of 400 eggs in the population studied could safely withstand rather high losses from the time of deposition to the time sexual maturity is attained.

SOCIAL RELATIONSHIPS

No aggressive encounters between *T. coahuila* were observed in the field, although individuals frequently foraged near one another. Four times I saw two or more *T. coahuila* in the same vicinity. Usually only one turtle was initially seen and watched, but when I moved forward to secure it, I found a second turtle nearby. Twice a male and a female were involved; in another instance a male was caught but the second individual escaped. On one occasion three turtles, all females, were within 3 meters of each other.

The limited evidence suggests no defense of a territory in nature, but frequent fights between *T. coahuila* have been noted in an outdoor enclosure at Arizona State University (W. L. Minckley, pers. comm.) Fighting in nature may not be as rare as suggested, but only difficult to observe, as Evans (1961) pointed out.

Evans (1956a, 1956b) reported aggressiveness and social hierarchies in captive *T. c. carolina*. Penn and Pottharst (1940) reported marked aggressiveness and fights among captive *T. carolina major*. In a laboratory study involving 13 *T. c. carolina* in two groups, Boice (1970) observed: (1) stable social hierarchies resembling those of more commonly studied vertebrates; (2) hierarchies accompanied by behaviors that ranged from pushing to biting; and (3) a potential for territoriality

exhibited by one sexually active male. These results were qualified, however: "the box turtle seems to prosper as a lethargic and independent animal . . . A social hierarchy did emerge when the turtles were encouraged to compete in unison but this is undoubtedly quite unlike most natural situations for *Terrapene*" (Boice 1970). No definite instances of intraspecific aggression were observed in the lengthy field studies of *T. o. ornata* (Legler 1960b), *T. c. carolina* (Stickel 1950), or *Pseudemys scripta* (Moll and Legler 1971).

SURVIVAL STATUS

Canals carrying water for irrigation destroyed one extensive aquatic habitat (Posos de la Becerra) in the basin in December 1964. The original surface area of this vast marsh-pool complex underwent an estimated reduction from about 10 km² to less than 0.2 km² (Cole and Minckley 1966), virtually eliminating the entire population of *T. coahuila* as well as populations of the other two endemic turtles, *Trionyx ater* and *Pseudemys scripta taylori*. I estimate the loss of marsh habitat by drainage at Posos de la Becerra to have been much less than 9.8 km², perhaps more realistically approaching ca. 0.25–0.50 km² (25–50 ha, as judged from maps of the basin and Fig. 16 in Minckley [1969]). If this revised surface area estimate is correct, and assuming a population density of 60 adult *T. coahuila* per acre (148/ha), ca. 3,700 to 7,400 *T. coahuila* may have died or emigrated.

The Survival Service Commission of the International Union for Conservation of Nature and Natural Resources (IUCN) defines a rare species as one "not under immediate threat of extinction [= *endangered* species], but occurring in such small numbers and/or in such a restricted or specialized habitat that it could quickly disappear." Although its prospects of survival presently do not seem to be in immediate danger, *T. coahuila* is certainly a potentially endangered species. On the basis of its specialized aquatic habitat and small geographic range within the surrounding Chihuahuan Desert, *T. coahuila* is best regarded currently as a rare species according to the IUCN definition.

Although other basin turtle species are larger, *T. coahuila* is, nonetheless, the largest and most conspicuous element of the reptilian fauna living in many of the small, shallow, spring-fed marsh communities in the Cuatro Ciénegas basin (where the other turtle species do not occur). Yet its precise role in the ecology of these marshes will remain largely unclarified until population productivity, as it relates to other organisms in the basin, both plant and animal, vertebrate and invertebrate, is better understood. *T. coahuila* appears to be an important animal within the

marsh community. Size, food habits, and population densities seem to bear out this view. Thus with density decrease of these turtles, it is reasonable to expect the shallow-water ecosystems of the basin to become altered in regard to their energetics, as well as their composition. More work is needed to clarify the ecological interrelationships existing between the unique biota of this basin, the *T. coahuila* population, and the physical environment.

Minckley (1969) warns that "acceleration of modification by man adds some urgency to the situation [in the Cuatro Ciénegas basin]. The biota is definitely under stress." Although habitat destruction appears to represent the major threat to its existence, *T. coahuila* could also be placed in jeopardy through callous exploitation by dealers in rare or unusual reptiles, or even by some herpetologists. Adequate series of *T. coahuila* have already been assembled; presently more than 100 preserved specimens are in U.S. museums alone. Hence there is very little need for future collecting, except when living specimens are required for valid experimental purposes.

No protective measures have yet been taken. In view of its rare status, I propose: (1) the adoption of measures to establish the feasibility of any planned irrigation projects in regions immediately surrounding the prime aquatic habitats in the Cuatro Ciénegas basin; (2) the establishment of restrictions against the indiscriminate construction of canals that may result in the drainage of major aquatic habitats; and (3) special protection for the animal itself in the form of legislation limiting collecting only for scientific purposes and by permission of the proper governmental authorities. Permission should be given only to investigators studying specific problems concerning the species.

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