

A PRELIMINARY ECOLOGICAL STUDY OF THE SOFT-SHELLED TURTLE *TRIONYX MUTICUS* IN THE KANSAS RIVER

HENRY S. FITCH AND MICHAEL V. PLUMMER
*Museum of Natural History, University of Kansas,
Lawrence, Kansas 66045, USA*

ABSTRACT

Trionyx muticus is abundant in the Kansas River, especially in sandy habitats. Egg-laying occurs chiefly in June and July and a female may produce two or more clutches per season. Clutches found in nests averaged 12.6 eggs. Nests averaged 38.2 m from the water and 1.34 m above the water level, and the average depth to the eggs was 16.2 cm. Eggs are approximately spherical, with a mean maximum diameter of 22.9 mm and a mean weight of 6.72 g. Hatchlings, emerging in late August and September, have an average carapace length of 34.84 mm and average weight of 4.91 g. By mid-June of the following year the hatchling cohort has gained 36% in length and 95% in weight. A crude estimate of population structure is made from the analysis of tracks left by basking turtles.

INTRODUCTION

The soft-shelled turtles of the genus *Trionyx* (Reptilia: Chelonia: Trionychidae) are an ancient and widespread group. They are known as far back as the Jurassic of France (Bergounioux, 1937; Webb, 1962). The several Recent species center their distribution within southeastern Asia, but with nearly continuous ranges across southern Asia eastwards to southeast and east Asia, west to Israel and Turkey, and south through much of Africa in the Nile and Congo basins (Webb, 1962). Four species well isolated from the others, but partly sympatric with each other, occur in North America.

The several species of *Trionyx* differ in size and markings and in details of their morphology, but are similar in general habits. All are highly aquatic. They often attain high population densities. In many areas they are prized as human food and they have even been farmed for this purpose. However, in the area of our study they are not eaten, but are considered pests because they sometimes interfere with fishermen's nets or lines. Those that are caught on hook and line are generally killed and discarded. These turtles are largely carnivorous, but are also scavengers, and take some plant food. They are of importance in local ecosystems.

Trionyx muticus Le Sueur, 1827, the subject of this study, is one of the smallest

Received 10 February 1974

Printed November 1975

species (usual carapace length of the female, about 180 mm (Carr, 1952)) but one that is widespread and ecologically important. It occurs in the Mississippi Basin including the entire Ohio River drainage of the eastern United States, the Missouri River drainage (except its northwestern part) and the Red River drainage of the southern Great Plains. Also, it occurs in several adjacent smaller river systems that empty into the Gulf of Mexico. Its entire geographic range is within that of the larger *Trionyx spiniferus*. However, in the area of our study *T. spiniferus* was found to be rare and *T. muticus* was extremely abundant. *T. muticus* is a plastic and variable species occurring over a wide range of climatic conditions and aquatic habitats. Despite Webb's (1962:541-578) review of the natural history of American *Trionyx*, the ecology of *T. muticus* remains little known.

This field study was initiated by Fitch in June 1970; it is being continued and expanded by Plummer whose participation began in July 1972.

MATERIALS AND METHODS

Our field study was made in 1970, 1971 and 1972 in the western part of the geographical range, a 60 km stretch of the Kansas River at approximately 39°N, from the vicinity of De Soto, Johnson County, Kansas upstream to the vicinity of Lecompton, Douglas County, Kansas. This study area was approximately 45 km upstream from the confluence of the Kansas and Missouri Rivers.

Where signs of activity indicated that the turtles were abundant, traps were set to capture them alive. The traps were of several designs and sizes including fyke nets and wire funnel traps. Captured turtles were individually marked by clipping notches in the margin of the shell, or by attaching colored bands or metal tags with serial numbers. In June and July field work concentrated on a search for nests in sandy places along the river or on its islands. They were found by digging in the sand to a depth of several inches. Discovery of nests was in part a matter of chance, but recognition of the types of situation preferred as nest sites, imprints of claws or shell in sand (often faint or obliterated) and loose consistency of sand filling the nest entrance were clues that often led to discovery of eggs. When nests with eggs were discovered, information such as distance from the river, height above water level, depth beneath surface of sand, and temperature of sand around eggs were recorded. The eggs were brought to the laboratory, measured, weighed and incubated. The hatchling turtles that emerged from them were likewise processed; they were group-marked, and were released in the general area where the nests had been found.

Occasionally, turtles were captured by hand, when the field workers were able to approach from behind screening vegetation or high banks, to observe the animals and then to run out and catch them before they could escape or conceal themselves effectively. Along the water's edge, widths of tracks were measured (from a line connecting outermost claw marks on one side to a similar line on the opposite side). From measurement of many (N = 66) turtles and their tracks, an attempt was made to correlate shell-length with track-width, and to determine composition of the local population by size classes. Much subjective judgment was involved, because where

tracks were abundant, with many of about the same width, leading to and from the water, it could not be definitely determined whether one individual or several were involved.

Statistical reductions are presented as the mean plus or minus one standard error.

RESULTS

Habitat

The turtles were found in and along the Kansas River and in the adjacent parts of tributaries but not in smaller streams. Although found over a wide range of habitats, they were most often associated with sand and swift current. They spend much of their time in the water but may emerge to bask or feed at the water's edge. Activity is concentrated, as shown by numerous tracks, where there are sandbars shelving off into deep and swift water. Basking is usually within 1 m of the water in exposed places.

The Kansas (or Kaw) River is a major tributary of the Missouri, and like other Great Plains streams its flow is highly variable. Amount and distribution of precipitation varies greatly, but in most years rainfall is greatest in June and July and minimal at the opposite time of year. Despite installation of dams to prevent flooding, the flow remains variable. Extensive areas of sandbars continuous for a kilometer or more at times of low water may at other times be completely inundated. The river bed, the flow of water and the amount of dissolved and suspended material is constantly changing, demanding adjustment on the part of the individual turtle.

General Behavior

In warm weather the turtles spend much time basking. They either emerge onto sand at the river's edge or onto emergent logs, or they lie submerged in water only a few cm deep warmed by the sun. Often such turtles embed themselves in shallow depressions so that the shell is partly or wholly covered by sand or silt. When the water level drops, large numbers of these circular depressions are in evidence just below the former shoreline. The turtles are alert and wary and their vision is keen. Ordinarily they detect an approaching person before they themselves are seen; they scuttle into the water and conceal themselves beneath the sand, or allow themselves to be swept away by the current. Small individuals may permit a person to approach within 30 m but large ones are much more wary.

Tracks and Composition of the Population

Accuracy of shell-length estimates based on track widths would doubtless be affected by the type of substrate, the weight of the turtle, its gait (running or walking), whether on land or partly immersed and buoyant, and the incline up or down a bank. Although we have not corrected for such variables, our data indicate that shell length can be determined with a fairly small margin of error from the width of the tracks. The ratio of length of plastron to width of track averaged approximately 0.90.

Through allometric growth the carapace changes from an almost round shape in hatchlings to an ovoid shape in adults (Muller, 1921; Webb, 1962), but there is corresponding change in the proportions of the plastron, so that the carapace/plastron ratio changes little with increasing size. For a sample of 164 turtles, the mean cara-

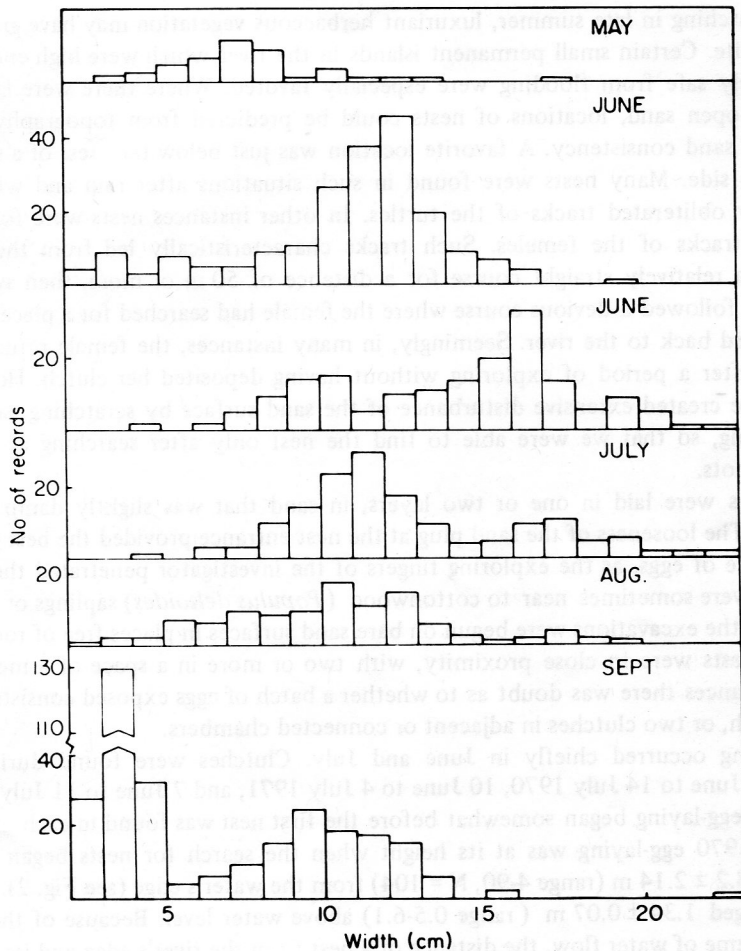


Fig. 1. Histogram depicting the widths of tracks measured on sandbars at different times of the year.

pace/plastron ratio was 1.38 ± 0.004 . For those near hatchling size ($N = 80$) the mean was 1.39 and for adults and large young ($N = 33$) the mean was 1.40, but for medium sized young, 40-59 mm ($N = 51$), the ratio was 1.34.

Figure 1 shows widths of tracks in series measured at different times. These do not show any well-defined trend, but most of the samples show at least two dominant age-size groups. Discrete size groups are lacking. The most striking aspect is the high proportion of hatchlings present in September 1970. Figure 1 is an index of basking activity. How closely this index represents true population structure remains to be determined in further work by Plummer.

Nests

Sandbars relatively free from vegetation were the preferred nesting areas but by the

time of hatching in late summer, luxuriant herbaceous vegetation may have grown up at a nest site. Certain small permanent islands in the river which were high enough to be relatively safe from flooding were especially favored. Where there were large expanses of open sand, locations of nests could be predicted from topography, vegetation and sand consistency. A favorite location was just below the crest of a sandbar on the lee side. Many nests were found in such situations after rain and wind had completely obliterated tracks of the turtles. In other instances nests were found by following tracks of the females. Such tracks characteristically led from the water inland in a relatively straight course for a distance of 50 m or more, then swerved, sometimes followed a devious course where the female had searched for a place to dig, and then led back to the river. Seemingly, in many instances, the female returned to the river after a period of exploring without having deposited her clutch. However, each female created extensive disturbance of the sand surface by scratching, scraping and tamping, so that we were able to find the nest only after searching at several different spots.

The eggs were laid in one or two layers, in sand that was slightly damp — not saturated. The looseness of the sand plug at the nest entrance provided the best clue to the presence of eggs, as the exploring fingers of the investigator penetrated the sand. The nests were sometimes near to cottonwood (*Populus deltoides*) saplings or weeds, but always the excavations were begun on bare sand surfaces in places free of roots.

Often nests were in close proximity, with two or more in a space of a meter. In several instances there was doubt as to whether a batch of eggs exposed consisted of a single clutch, or two clutches in adjacent or connected chambers.

Egg-laying occurred chiefly in June and July. Clutches were found during the periods 25 June to 14 July 1970, 10 June to 4 July 1971, and 7 June to 11 July 1972. Doubtless, egg-laying began somewhat before the first nest was found in each of these years. In 1970 egg-laying was at its height when the search for nests began. Nests averaged 38.2 ± 2.14 m (range 4-90, $N = 104$) from the water's edge (see Fig. 2). These nests averaged 1.34 ± 0.07 m (range 0.5-6.1) above water level. Because of the fluctuating volume of water flow, the distance of a nest from the river's edge and its height above the water would often have changed between the time of deposition and the time of discovery by us. However, in most instances the time interval was short and the change probably was a relatively minor one. Depth from the sand surface to the tops of the eggs averaged 16.2 ± 0.38 cm (range 7.6-25.4, $N = 95$).

Nesting areas were often recognized as such by the remains where the nests had been destroyed by carnivores. Dogs, coyotes (*Canis latrans*), striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) all preyed upon the eggs judging from the numerous tracks in the areas where nests were destroyed. For instance, on 7 June 1972 on a sandbar two miles north of Eudora, 12 intact nests were found within approximately 200 m and 16 other nests had been dug out or destroyed by predators. In most instances it seemed that the eggs had been located by scent soon after laying. The coyote was suspected of being one of the most important predators locally because of its numerous tracks on the sandbars where eggs were found. On small islands nests were relatively free from predation. At nests where most of a clutch had been

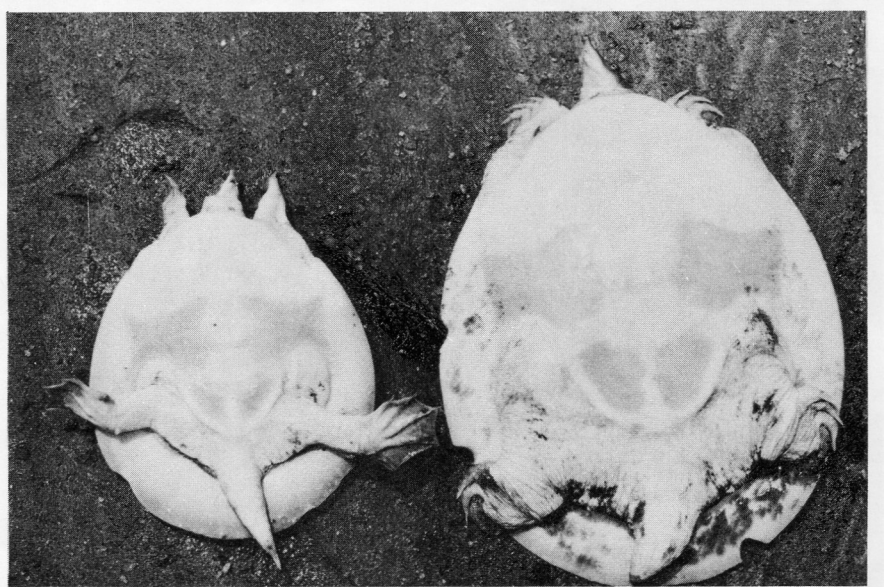
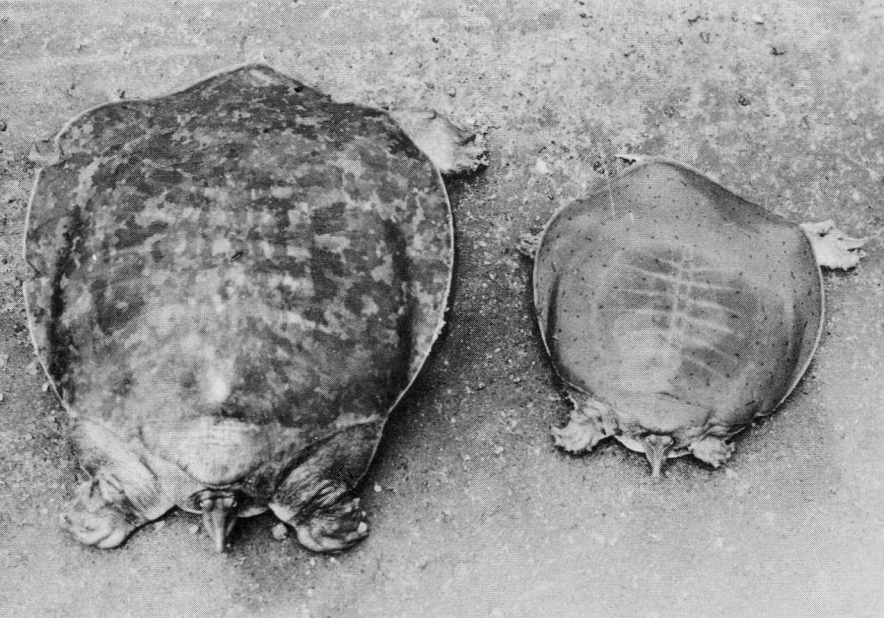


PLATE I

Trionyx muticus, adult female and male, showing differences in size, proportions and markings. Notches in margins of shells are marks for individual identification. Specimens from Kansas River, Douglas County, Kansas, 6.VI.1974. Top - dorsal aspect, female on the left.

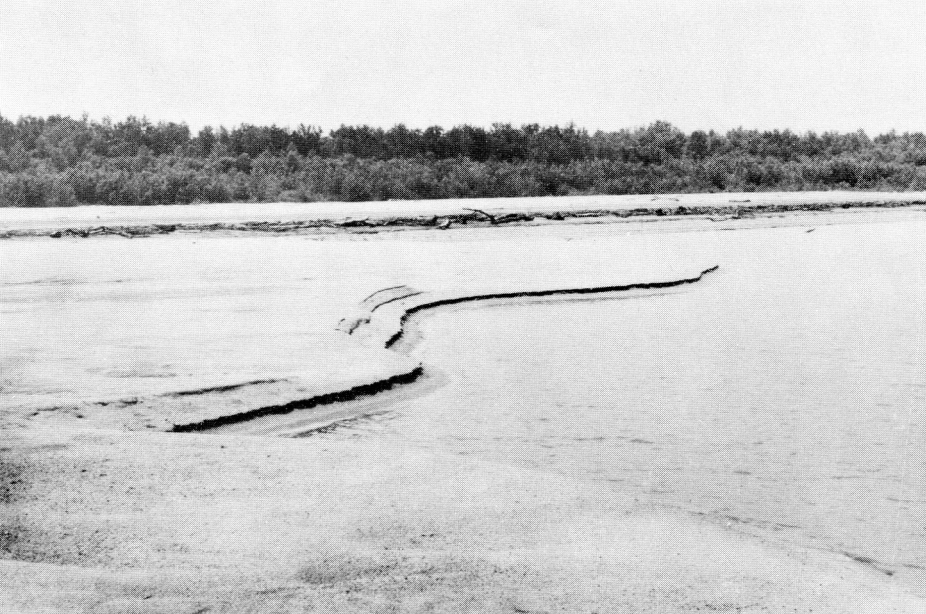




PLATE II

Habitat of *Trionyx muticus* at Kansas River, Douglas County, Kansas, 6.VI.1974. Top - sandbar with steep banks adjacent to deep, swift water (basking place for many of the turtles). Bottom - extensive sandy area 4 km east of Lawrence, exposed by receding water.





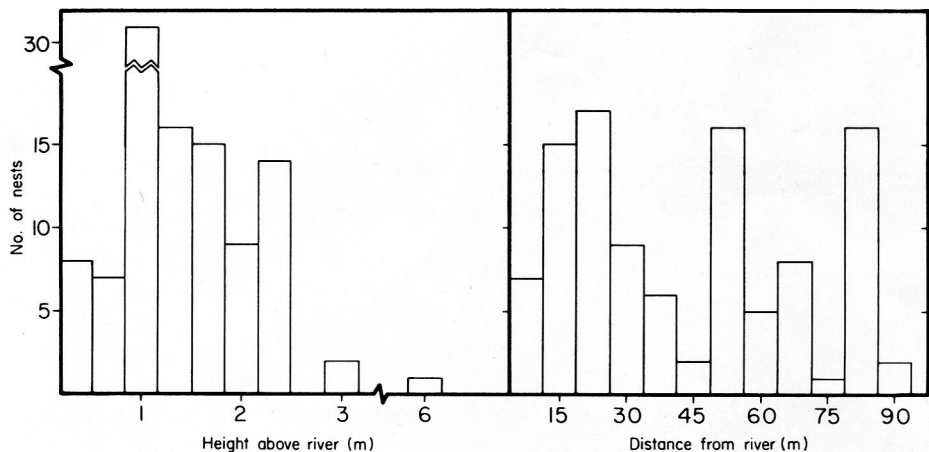


Fig. 2. Frequency distribution of the number of nests found at various heights above water level and at various distances from the water's edge.

destroyed, one or more intact eggs often remained. Evidently some such eggs were overlooked because they were on the side of the nest chamber farthest from where the predator broke in. Sand collapsing into the nest chamber and above it served to conceal and protect such overlooked eggs; some of them may have survived and eventually hatched. In other cases, an egg was thrown out with the sand by the digging predator, and because of its spherical shape, rolled away, often to a distance of a meter or more where it escaped notice. Several nests which showed no disturbance on the surface were penetrated by tunnels of the mole (*Scalopus aquaticus*), and fragments of eggshell remained, indicating that the eggs had been eaten. Perhaps some were carried away by the mole. For some nests that had been destroyed, it was possible to obtain a tentative count of the number of eggs from the empty shells. In most instances the eggs had been chewed, and perhaps some of them had been swallowed entire judging from the paucity of the remains.

Since the turtles do not venture far from the water for egg-laying, every nest is subject to the potential hazard of flooding and this is probably a major cause of mortality before hatching. Eggs can survive brief immersion, depending on stage of development, water temperature, and other circumstances, but during their incubation, an extended rise of even a few inches such as occurs after heavy precipitation can destroy many nests. Flora (1948) recorded that in an 18-year period (1927-45) the Kansas River overflowed its banks 23 times. Presumably such overflows, and even much smaller rises in water level, destroy all or most of the incubating eggs. For the 23 floods that Flora recorded, seasonal distribution was as follows: one in March, two in April, five in May, nine in June, one in July, two in August, two in October, one time unrecorded. Six of the nine June floods came in the earlier half of the month. Thus, from the peak of the laying season onward, the average trend is toward lower water levels.

The last major flood was in July 1951 when the Kansas River overflowed its banks

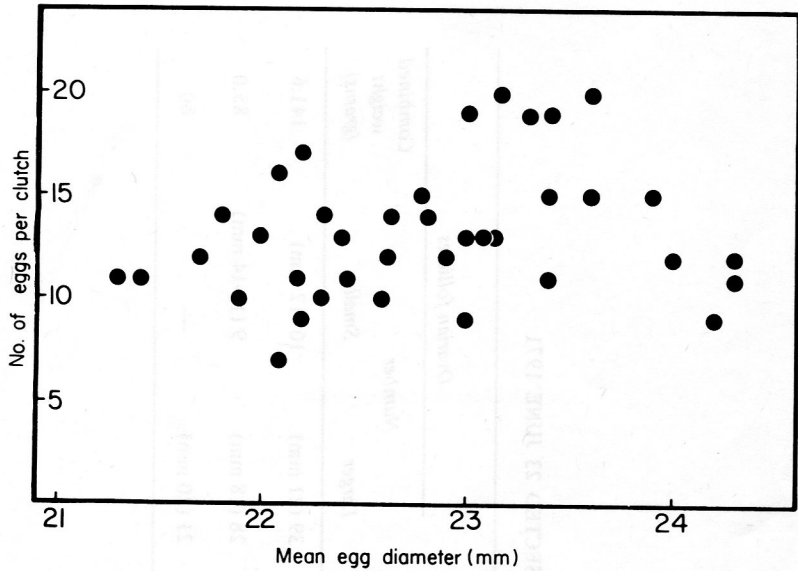


Fig. 3. The relationship of mean egg diameter to the number of eggs in a clutch.

and spread over its entire flood plain. Since the floods that Flora recorded, impoundments have been installed on all major tributaries, at Cedar Bluff, Glen Elder, Kanapolis, Kirwin, Milford, Lovewell, Morton, Perry, Tuttle Creek, Webster and Wilson, and flooding has been largely brought under control. After heavy precipitation, runoff is stored in the reservoirs and released gradually, preventing the river from either overflowing its banks or shrinking to an extremely low level in time of drought. Relatively small scale fluctuations in water level still occur, however, and egg-laying sites are flooded at times. Artificial control of the river's flow undoubtedly results in greater security and a higher survival rate for the nests.

Eggs

Size and shape. The eggs tend toward spherical shape and have white, calcareous, hard but fragile shells. Within any one clutch, eggs tend to be relatively uniform in size and shape. From an elliptical shape of 24×19.5 mm at one extreme, eggs varied toward almost perfect spheres. Diameters averaged 22.9 ± 0.04 mm for 463 eggs of 38 clutches measured in 1972. Eggs collected in June averaged (23.0 ± 0.05 mm) slightly larger than those collected in July (22.1 ± 0.08 mm) but the difference is not significant. Average weight was 6.72 ± 0.04 g ($3.4-9.0$) in 439 eggs of 38 clutches. In Fig. 3, egg diameter plotted against number of eggs per clutch shows lack of correlation.

Number per clutch. For the three seasons of field work, clutches averaged 12.6 ± 0.30 eggs ($N = 199$). The separate means for the three years did not differ significantly but clutches collected in June ($N = 96$) averaged (13.4 ± 0.40) larger than those collected in July (11.8 ± 0.43 , $N = 103$). This difference is significant at the $P = 0.01$ level. Perhaps for any given female, the first clutch of the season, usually laid in June,

TABLE I
NUMBERS OF EGGS IN GRAVID FEMALES DISSECTED 23 JUNE 1971

| Individual | Shell length and weight of turtle | | Shelled eggs | | | Ovarian follicles | | |
|------------|-----------------------------------|---------------|----------------|--------|-------------------------|-------------------|--------------|-------------------------|
| | Carapace (mm) | Plastron (mm) | Weight (grams) | Number | Combined weight (grams) | Larger | Smaller | Combined weight (grams) |
| No. 1 | 240 | | 1274 | 23 | 141.6 | 39 (21 mm) | 10 (12 mm) | 141.6 |
| No. 2 | 235 | 173 | 1056 | 14 | 106.7 | 28 (18 mm) | 9 (10-14 mm) | 85.0 |
| No. 3 | 218 | 156 | 945 | 12 | 102.5 | 21 (20 mm) | — | 80 |

is larger than the second or third clutch, usually laid in July, but we obtained some evidence to the contrary.

Table I shows numbers and sizes of eggs in three ovigerous females, each caught where it had excavated a nest cavity, no. 1 on 3 June and nos. 2 and 3 on or about 10 June. Although obviously prepared to oviposit, all three retained their eggs when held in confinement, even when provided with a quantity of damp sand suitable for nesting. No. 1 laid two eggs on 10 June after a week of confinement, and laid a third egg on 12 June but retained the remainder of her clutch. Besides the shelled eggs that they were about to lay when captured, each female contained a greater number of large ovarian follicles that probably would have formed additional clutches. These clutches would have totalled 1.8 times as many eggs as the first clutches, with remarkably large numbers of follicles, 39 and 28, seemingly destined to form clutches. Size was notably uniform in these follicles. The two largest females also had series with 10 and 9, respectively, of half-sized follicles.

Figure 4 shows frequency distribution of number of eggs per clutch in the 201 nests examined in the three seasons of field work. It shows that most nests have nine to 15 eggs with 12 as the most frequent number. Some clutches deviate markedly from the usual clutch size, and the significance of this deviation cannot be determined. In clutches having fewer than the usual numbers of eggs, it may be suspected that the female had distributed her clutch between two or more nests. Such distribution seemingly occurs in the tropical trionychid, *Lissemys punctata*. In Ceylon, Deraniyagala (1939) found two to five eggs, average 2.86 in seven *Lissemys* nests but found 11 shelled eggs plus 18 large follicles in a female that was dissected. In *Trionyx* nests, unusually large batches of eggs may be suspected as composites representing the combined efforts of two or more females.

However, the dissections of ripe females indicated that clutches having more than 20 eggs are not rare and that the usual sized clutches of nine to 15 eggs found in nests do not represent the full complement; a female may sometimes divide her clutch

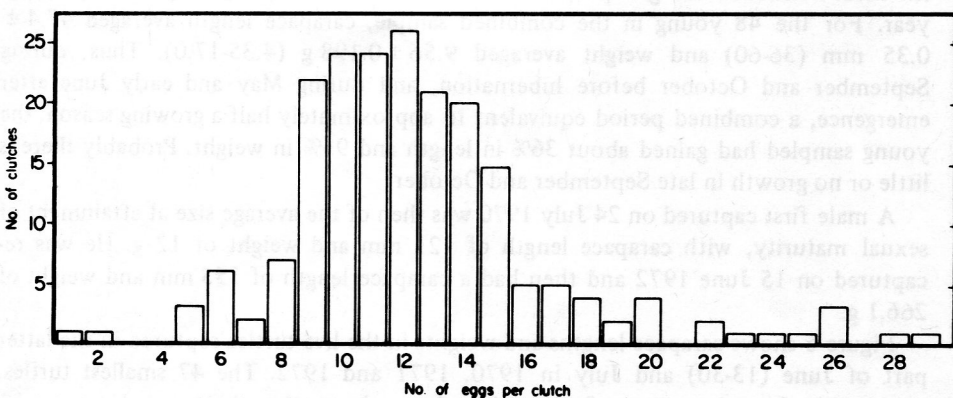


Fig. 4. Frequency distribution of the number of eggs per clutch for 201 nests examined in three seasons of field work.

between two nests. Eight unlaidd clutches in three females averaged 19.5 eggs, 55% more than the clutches found in nests, and four of the eight greatly exceeded the usual complements found in nests, with 21, 23, 28 and 39 eggs (Table I).

The relationships of nest size, clutch size, and number of clutches per female per season in this population of *T. muticus* remain unclear and are currently being investigated further.

Webb (1962:570-571) cited records of number of eggs per clutch in 36 clutches of *Trionyx muticus*. In 24 clutches from Illinois, Missouri and Iowa at a latitude of approximately 40°N, the clutches averaged 18.36 (4-33 eggs). Twelve clutches from more southern latitudes (below 36.5°N) averaged 7.3 (3-15). Webb found a similar trend in *Trionyx spiniferus*. He suggested that in northern populations the eggs are smaller with more per clutch and only one clutch per season, whereas in southern populations the eggs are larger and fewer per clutch with three clutches per female in a season.

Somewhat similar geographic trends have been observed in other North American freshwater turtles. Tinkle (1961:75) found that in the northern United States (Connecticut, Illinois, Kansas, Maryland, Michigan, New Jersey, New York, Pennsylvania) mean clutch size for *Sternotherus odoratus* was 4.6 eggs, but in southern states (Alabama, Arkansas, Florida, Georgia, Louisiana, Tennessee, Texas) the mean was 4.2 and eggs averaged larger. Cagle (1954) found a mean clutch size of 6.3 eggs in *Chrysemys picta* in Illinois, but found a mean of only 4.3 in Tennessee. In *Pseudemys scripta*, Cagle (1950) found an average clutch of 9.3 in Illinois, 10.5 in Tennessee and 7.0 in Louisiana, but Moll and Legler (1971:31) found an average of 17.4 eggs in the much larger turtles of this species occurring in the tropics of Panama.

Growth

In 100 hatchlings measured in late August 1970, length of carapace averaged 34.84 ± 0.225 mm (30.1-39.2) and weight averaged 4.91 ± 0.33 g (2.9-7.3). On 13 June 1971 and 15 June 1972, sizable samples of live turtles were obtained, in which the most numerous size group was small and seemed to be the young of the previous year. For the 48 young in the combined sample, carapace length averaged 47.4 ± 0.35 mm (36-60) and weight averaged 9.56 ± 0.198 g (4.35-17.0). Thus, during September and October before hibernation, and during May and early June after emergence, a combined period equivalent to approximately half a growing season, the young sampled had gained about 36% in length and 95% in weight. Probably there is little or no growth in late September and October.

A male first captured on 24 July 1970 was then of the average size at attainment of sexual maturity, with carapace length of 121 mm and weight of 12 g. He was recaptured on 15 June 1972 and then had a carapace length of 155 mm and weight of 266.1 g.

Figure 5 shows carapace lengths and weights in the live turtles captured in the latter part of June (13-30) and July in 1970, 1971 and 1972. The 47 smallest turtles, presumably first-year young, form such a dense cluster that their records cannot be shown individually. From the increase over hatching size in these first year young,

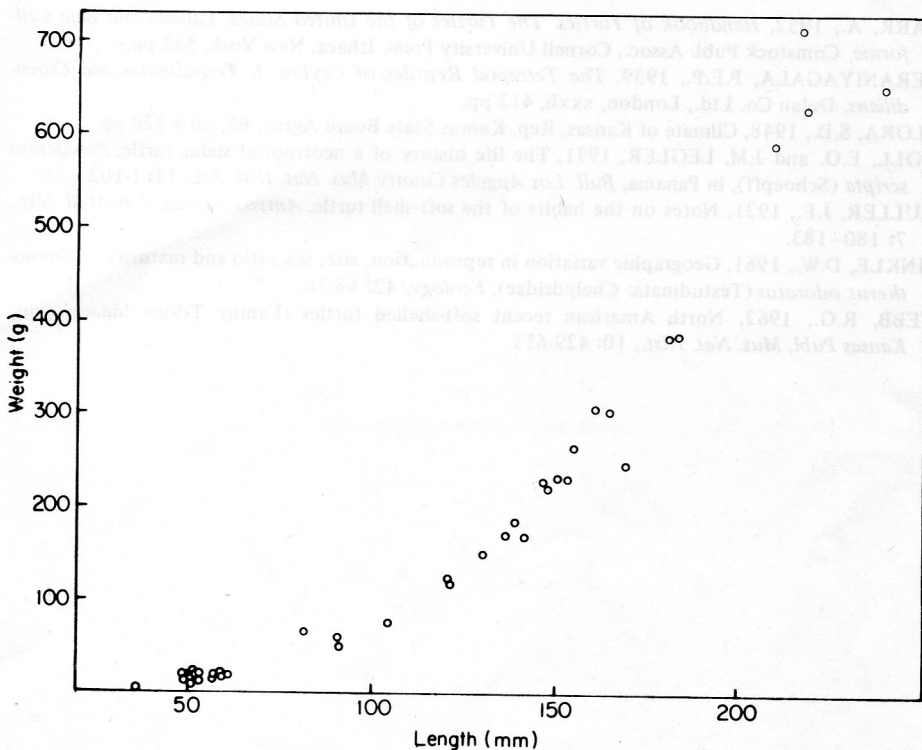


Fig. 5. The relationship of body weight to carapace length in *Trionyx muticus*.

from the clustering of records of larger young, and from Webb's (1962:575) description of growth in marked populations of *T. sinensis* and *T. spiniferus* it is suggested that most of the remaining turtles are second through fifth year individuals.

ACKNOWLEDGMENTS

We thank Jananne Bishop Hall, Mark Cain, Matthew Cain, Michael D. Cain, Chester W. Fitch, Richard K. Lattis, Arnold K. Smith, Roxanne Smith, Pennie L. von Achen and Larry Watkins for assistance in the field. The Cain brothers, especially, captured many live turtles for us, located many nests, and provided us with information regarding the habits and local distribution of the turtles which served as the basis for our study.

REFERENCES

- BERGOUNIOUX, M.F.-M., 1937, Cheloniens fossiles du Kimeridgien du cap de la Heve, *Bull. Soc. Nat. Hist. Toulouse*, 71: 180-191.
- CAGLE, F.R., 1950, The life history of the slider turtle, *Pseudemys scripta troosti* (Holbrook), *Ecol. Monogr.*, 20: 31-54.
- CAGLE, F.R., 1954, Observations on the life cycles of painted turtles (Genus *Chrysemys*), *Am. Midl. Nat.*, 52: 225-235.

- CARR, A., 1952, *Handbook of Turtles. The Turtles of the United States, Canada and Baja California*, Comstock Publ. Assoc., Cornell University Press, Ithaca, New York, 542 pp.
- DERANIYAGALA, P.E.P., 1939, *The Tetrapod Reptiles of Ceylon. I. Testudinates and Crocodylians*, Dulau Co. Ltd., London, xxxii, 412 pp.
- FLORA, S.D., 1948, *Climate of Kansas*, Rep. Kansas State Board Agric., 67, xii + 320 pp.
- MOLL, E.O. and J.M. LEGLER, 1971, The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama, *Bull. Los Angeles County Mus. Nat. Hist. Sci.*, **11**: 1-102.
- MULLER, J.F., 1921, Notes on the habits of the soft-shell turtle, *Amyda mutica*, *Am. Midl. Nat.*, **7**: 180-183.
- TINKLE, D.W., 1961, Geographic variation in reproduction, size, sex ratio and maturity of *Sternotherus odoratus* (Testudinata: Chelydridae), *Ecology*, **42**: 68-76.
- WEBB, R.G., 1962, North American recent soft-shelled turtles (Family Trionychidae), *Univ. Kansas Publ. Mus. Nat. Hist.*, **10**: 429-611.

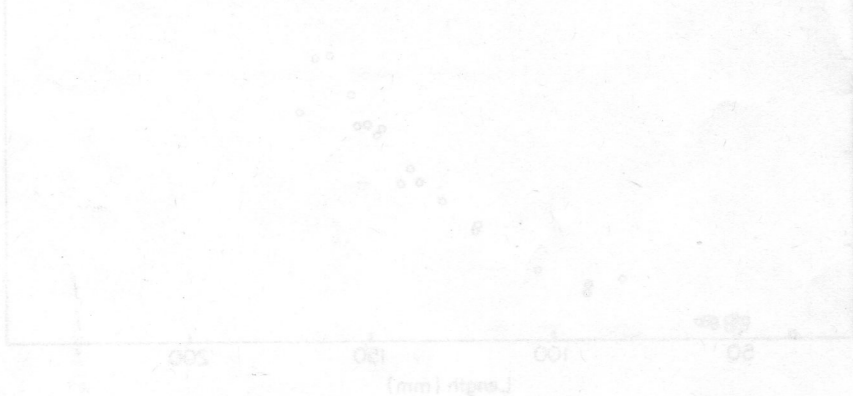


Fig. 1. The relationship of body weight to carapace length in *Pseudemys scripta*.

from the clustering of records of larger young and from Webb's (1962:575) description of two marked populations of *V. carolinensis* and *V. floridana* it is apparent that most of the remaining turtles are second through fifth year individuals.

ACKNOWLEDGMENTS

We thank James Bishop, Bill Hall, Mark Cain, Matthew Cain, Michael D. Cain, Chester W. Pritchard, Richard K. Eattie, Arnold K. Smith, Roxanne Smith, Pierre L. van Arman and Gary Watkins for assistance in the field. The Cain brothers, especially, captured many turtles for us, located many nests, and provided us with information regarding the sites and local distributions of the turtles which served as the basis for our study.

REFERENCES

- BERGQUIST, M. F. M., 1937, *Chelonian faunas in Florida*, *Florida Geologist*, **12**: 1-10.
- CARR, A., 1952, *Handbook of Turtles. The Turtles of the United States, Canada and Baja California*, Comstock Publ. Assoc., Cornell University Press, Ithaca, New York, 542 pp.
- FLORA, S. D., 1948, *Climate of Kansas*, Rep. Kansas State Board Agric., 67, xii + 320 pp.
- MOLL, E. O. and J. M. LEGLER, 1971, The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama, *Bull. Los Angeles County Mus. Nat. Hist. Sci.*, **11**: 1-102.
- MULLER, J. F., 1921, Notes on the habits of the soft-shell turtle, *Amyda mutica*, *Am. Midl. Nat.*, **7**: 180-183.
- TINKLE, D. W., 1961, Geographic variation in reproduction, size, sex ratio and maturity of *Sternotherus odoratus* (Testudinata: Chelydridae), *Ecology*, **42**: 68-76.
- WEBB, R. G., 1962, North American recent soft-shelled turtles (Family Trionychidae), *Univ. Kansas Publ. Mus. Nat. Hist.*, **10**: 429-611.