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SOME ASPECTS OF NESTING SUCCESS IN THE TURTLE, *TRIONYX MUTICUS*¹

MICHAEL V. PLUMMER

ABSTRACT: Nesting success of the midland smooth softshell, *Trionyx m. muticus*, was studied in Kansas during two field seasons from individually marked nests. Supplementary information was obtained from eggs subjected to submersion experiments in the laboratory. Open areas on high ridges of sandbars were preferred nesting sites; apparently ♀♀ recognized these areas from the water. The major cause of egg mortality was submersion resulting from extended rises in water level. Nesting success was lower in 1973, an unusually wet season, than in 1974 which was unusually dry.

FRESHWATER turtles are long-lived animals characterized by low mortality in adults, but often with high mortality in embryonic and hatchling stages (Allen, 1938; Cagle, 1950; Gibbons, 1968; Moll and Legler, 1971; Wilbur, 1975; Burger, *In press*). The major source of mortality often is predation on the eggs and hatchlings. Other factors, such as desiccation, temperature extremes, hypo- or hyperosmotic medium, and flooding undoubtedly cause some mortality in eggs and hatchlings; some of these may be of major importance in certain situations. For example, Ragotskie (1959) attributed mortality in 15 *Caretta* nests to excessive rainfall. Entire broods of *Podocnemis* may be killed by rising water levels during a premature wet season (Roze, 1964).

In river populations of *Trionyx muticus*, females nest relatively close to water on sandbars, thereby exposing the eggs to possible inundation from the rapid and frequent fluctuations in water level characteristic of lotic environments (Fitch and Plummer, 1975). In 1973 the Kansas River reached its highest levels since a major flood in 1951 when the entire floodplain was covered. In contrast, 1974 was unusu-

ally dry and water levels remained low and stable. This paper reports on the nesting success of *T. m. muticus* associated with the contrasting fluctuations in water level of the 2 years.

METHODS

Field Study.—The study area was a sandbar in the Kansas River, Douglas County, Kansas, USA, which normally was exposed for a distance of 1–1.5 km depending on the water level. Permanent vegetation (primarily saplings of cottonwood, *Populus deltoides*, and sandbar willow, *Salix interior*) occurred proximally to the relatively permanent shoreline. Distally, the sandbar was free of vegetation except for plants which became established in certain areas (primarily on the lee end where silt content was high) in between scourings of the sandbar by high water (see Plummer and Shirer, 1975, Fig. 3 for aerial photograph). The study area was searched at least once each day from mid-May through July (1973–1974) for signs of nesting activity. Most nests were found by following tracks of nesting females initially located near the water's edge. When a nest was located its approximate distance from water, distance from vegetation, height above water, and longitudinal

¹ This paper is a portion of a Ph.D. dissertation submitted to the faculty of the Department of Systematics and Ecology, University of Kansas.

placement on the sandbar were noted. The nature of the substrate also was noted; the eggs were counted and carefully replaced and re-covered in their original position, and the width of track leading to the nest was measured. A numbered tag was affixed to a flagged stake of stiff wire inserted into the sand near the nest. Each nest location was checked daily until hatching, or if hatching did not occur when expected the eggs were dug up to determine their condition. The number of eggs hatched was determined from the number of empty eggshells present in the nest.

A water level gauge was installed 2 km upstream from the study area. Fluctuations in water levels permitted contour mapping of the sandbar, and from these measurements a lateral profile was determined each year; minor changes in the profile also were noted after water rises. The sandbar was staked in 100-m lengths for longitudinal measurement.

Experimental.—Seventy-five clutches were collected in 1974 from sandbars 2–6 km downstream from the study area for laboratory experiments. The eggs were carefully removed from nests, transported to the laboratory and placed in plastic shoeboxes for incubation. Eggs were placed in each box in a single layer on a shelf of wire mesh which was covered with Dacron® polyester fiber. A small amount of water was maintained in the bottom of each box; they were covered and kept in a well-ventilated room with temperatures determined by outdoor air temperatures (approximate range, 18°–40°C; average ≈ 28°C).

Some 676 eggs from 59 clutches collected over 12 days in early June were used for submersion experiments. Each egg was randomly assigned (after all eggs were collected) to one of eight different boxes (≈ 84 eggs/box), two of which were controls for incubation without submersion; in six others eggs were submersed for periods of 12 hours to 15 days. All eggs were collected within 1 day after laying and were incubated until assignment. Because each egg

was randomly assigned, each box held a random sample with regard to clutches and to amount of incubation (1–12 days) at the beginning of the submersion experiments. Some 154 eggs from 16 other clutches were maintained as integral units and were incubated without submersion in boxes (≈ 51 eggs/box) with individual eggs of a clutch in contact with each other. Contingency table analysis and the methods of Sokal and Rohlf (1969) were used to analyze the proportional data obtained from these experiments.

Hatchlings obtained from these experiments were marked and released in the Kansas River in the general area where the eggs were collected.

RESULTS AND DISCUSSION

Climatic.—Greater local precipitation and higher, more variable water levels in 1973 contrasted sharply with less precipitation and low, stable water levels in 1974 (Fig. 1). Water level was not directly correlated with local rainfall; it was primarily determined by output from various dams.

Numbers of Nests.—Thirty-nine nests were found within a day after laying in 1973. Nine other nests, located in late summer by backtracking hatchlings, were all far from the water at relatively high levels within permanent vegetation. Thirty-eight nests were located within a day after laying in 1974. Seventeen others were located in late summer by following hatchling tracks, two of which were located far from the water at high levels within permanent vegetation. Because nests located on the open sandbar in 1973 did not hatch, the chances of finding such nests by following hatchling tracks was nil that year. In 1974 such nests were notably successful. Thus, approximately equal effort in nest search in the 2 years yielded 48 and 40 nests, respectively (excluding nests found by backtracking hatchlings on the open sandbar in 1974).

Nesting was recorded on 7 June in 1973 and on 27 May in 1974. The last nest found immediately after construction was on 17

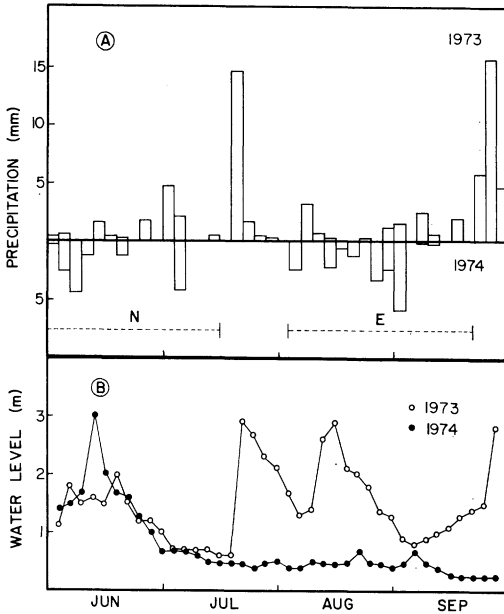


FIG. 1.—A = rainfall at Lawrence, Kansas. Each bar represents the mean of a 3-day period. Source: U.S. Weather Bureau Climatological Data, Kansas Section. Dashed line indicates times of nesting (N) and emergence of hatchlings (E) of *Trionyx muticus*. B = water level of the Kansas River near study area. Each point represents the mean of a 3-day period.

July in 1973 and on 9 July in 1974. Therefore, by the criterion of location of fresh nests the nesting seasons of 1973 and 1974 lasted 40 and 44 days, respectively.

Nesting Behavior.—Muller (1921), Cahn (1937), Goldsmith (1944), and Fitch and Plummer (1975) recorded original observations on nesting behavior in *T. muticus*. I observed that only 11% of the nests were constructed on overcast or rainy days. Over 72% of the nests that were constructed during fair weather were constructed during the first 3 days after overcast or rainy weather. Although the study area was searched every day during the nesting season, it would have been possible to overlook nesting in heavy rain because of obliteration of tracks; however, nesting usually was not seen for several overcast, rainless days before or after precipitation. Similar concentration of nesting in fair weather has

been noted in *Malaclemys* (Burger and Montevecchi, 1975).

Females often burrowed immediately after completion of their nests. Their activity formed shallow troughs with the nest in one end and the female in the other. Most of the troughs were straight and <1 m long but one was \approx 4 m and followed a sinuous course. Harper (1926) recorded the observations of A. Chesser who noted that nesting softshells (probably *T. ferox*) often burrowed before returning to water.

Nest Site Preference.—Ninety percent of the nests were constructed on open sandbar in areas free of vegetation, but in certain areas subsequent growth of vegetation shaded the nests and infested them with root growth. During periods of high water turtles nested in small patches of sand among dense, permanent vegetation. Similar observations on nest site preferences have been made by Goldsmith (1944), Anderson (1958), Webb (1962), and Fitch and Plummer (1975).

Water currents molded sandbars with extensive flat areas that gradually sloped up to a ridge and then abruptly sloped down to another flat. The resultant one or more high ridges were oriented at an angle to the shoreline. Nests were clumped at the highest points (ridges) on the lateral profile of the sandbar (Fig. 2). Severe flooding during the winter of 1973–1974 shifted the main high ridge of the sandbar downstream \approx 400 m. A corresponding shift of nesting density followed in 1974.

In Fig. 2 the distribution of emergence points of large females which wandered on the sandbar but did not oviposit are compared to the distribution of actual nests in the same season. Correspondence is close considering the entire length of the sandbar, much of which was not used by nesting turtles. Apparently turtles are able to see and select suitably high areas while still in the water. Wandering of females on sandbars probably involves search for suitable medium for oviposition, and not with longitudinal searching for high ridges.

Fate of Nests.—Once in the nest, a clutch

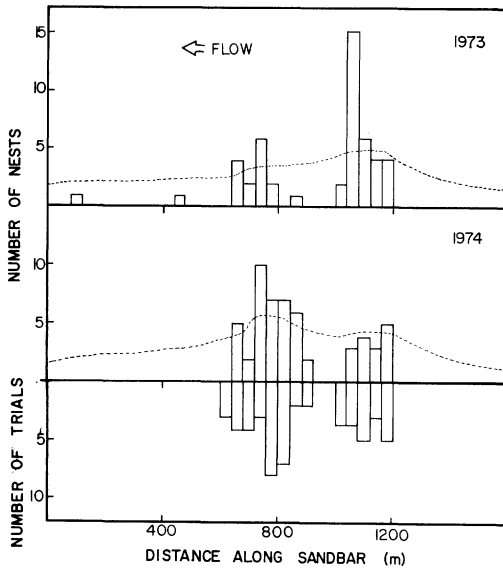


FIG. 2.—Distribution of *Trionyx muticus* nests at the study area for 1973 and 1974 in relation to simplified longitudinal profile of sandbar (dashed line), and to distribution of 1974 emergence points of large ♀♀ which wandered on the sandbar (nesting trials) but did not oviposit.

is subject to various hazards; examples include siltation, predation, erosion and destruction by rainwater (if laid on a steep slope), washing out and destruction by currents with rapidly rising river water, and sufficient inundation to kill the embryos. In 1973 only 2% of the eggs in nests that were located at the time of oviposition eventually hatched whereas 49% of such eggs hatched in 1974.

In 1973 a large sandbar 6 km downstream from the study area had a higher number of nests than any other known sandbar. Likewise in the early part of the nesting season in 1974 there was much nesting activity there, but a brief increase in water level deposited thick layers of silt. After the water receded, nesting tracks were abundant, but no further nesting occurred. The clutches laid earlier either failed to develop or the hatchlings were unable to emerge through the hardened layer.

Canids attacked seven nests on the study

TABLE 1.—Comparison of the fates of intact nests of *Trionyx m. muticus* for 2 years.

	Length of inundation (days)	Nests (n)	Eggs (n)	Eggs hatched (n)	hatched (%)
1973	0	2	18	2	11.1
	1-2	2	26	0	0
	3-5	4	48	7	14.6
	6-10	3	26	0	0
	> 10	17	171	0	0
1974	0	27	255	177	69.4
	1-2	5	64	32	50.0

area in 1973 and two in 1974. Considerable intervals (1-7 weeks) elapsed between oviposition and predation. Rising water levels washed out three nests in 1973 and four nests in 1974; rainwater washed out one nest in 1973. The remainder of the nests remained intact and were subject to different fates as summarized in Table 1. A major difference in survival between the 2 years is correlated with different periods of inundation. Most of the 1973 nests were inundated for 2-12 days after the water level rose on 20 July (see Fig. 1). Other periods of inundation began on 9 August and 24 September. Low survival in 1973 and high survival in 1974 with little inundation suggests that periods of inundation of only a few days damage or destroy *T. muticus* eggs; this hypothesis is supported by laboratory experiments, at least in early developmental stages.

It is possible that a few of the nests in Table 1 suffered deleterious effects from factors other than inundation. For example, two 1974 nests laid in dense, permanent vegetation were shaded, became invaded by roots, and did not hatch. One nest (9 eggs) was not inundated; the other (15 eggs) was inundated for ≈ 36 h, 3 days after it was laid. This nest contained 11 eggs that showed no development and 4 dead late-term embryos. Whether egg death in these nests was caused by inundation, increased water retention by the silty media after precipitation, root invasion, lowered temperatures caused by shading, or to some other factor could not be deter-

TABLE 2.—Comparison of various parameters for laboratory and field clutches of *Trionyx m. muticus* in 1974.

Group	Clutches (n)	Eggs (n)	Hatched (%)	Infertile or early inviable (%)	Died in shell (%)	Mean incubation or emergence (days)
Laboratory	16	154	60.4	31.8	7.8	49 ± 2.4
Field	32	319	63.3	26.0	10.7	68 ± 1.4

mined. Likewise, the four 1973 nests which suffered no inundation or 1–2 days inundation and had low success were deposited in silty media near permanent vegetation.

Experimental.—In incubation experiments the possible effects on the eggs of handling, of relatively more constant temperature and moisture regimes, and of high density of eggs within closed containers should caution the direct comparison to field results. Some eggs apparently absorbed sufficient moisture to enlarge the egg and expose areas of egg membranes where the calcareous shell had cracked and the fragments had drawn apart. Such enlargement and fragmentation occurs in natural nests late in incubation, but not to the extent that it occurred in the laboratory. When eggs were submersed, the water was not changed until treatments ended. Metabolic heat from incubating turtle eggs may raise nest temperature several degrees over ambient (Bustard and Greenham, 1968). In laboratory containers metabolism could raise the temperature of the water and deplete its O₂ content, but in natural nests rising water level usually is associated with slightly lower temperatures and higher O₂ content, possibly promoting longer survival of the eggs.

Despite such differences for eggs incubated in the laboratory and in the field, results are somewhat similar. Percentage of eggs hatched, of those showing no development, and of those having well-formed turtles which died before hatching in field clutches and laboratory controls are compared in Table 2. Incubation times for field clutches were not obtained because after initial processing, I avoided re-opening nests in order to minimize disturbance.

No significant difference from the control groups in percentage of eggs hatched occurred until eggs were submerged for 2 days (Table 3). The decline from the 12-h group to the 24-h group is not significant nor is that from the 24-h group to the 2-day group but the probability is low ($P < .07$) that this decline occurred by chance alone. These data suggest that in early embryonic stages, chance of surviving after submersion > 24 hours is less than with no submersion; increasing lengths of submersion result in decreasing survivorship; and after submersion > 4 days there is little chance of surviving.

The difference in percentage of eggs hatched in the laboratory control group (60.4%) and in the two control groups in the experiment (46.0% and 38.4%, respectively) is difficult to explain. Differences in treatment included laboratory control clutches maintained as integral units, whereas in the controls of the experiments the eggs were freely mixed and randomly assigned. Also, density of eggs in the boxes

TABLE 3.—Results of submersion experiments on eggs of *Trionyx m. muticus*. Vertical lines are maximum nonsignificant subsets.

Treatment	Eggs (n)	Hatched (n)	Hatched (%)
Control	87	40	46.0
"	86	33	38.4
12 hours	83	32	38.6
24 "	85	29	34.1
2 days	86	16	18.6
4 "	82	10	12.2
8 "	84	3 ^a	3.6
15 "	83	0	0

^a Eggs were clumped together in corner of box and protruded out of water for an undetermined period.

was lower in the control clutches. Possibly gas exchange was stressed under high density conditions.

Emergence.—Small depressions in the surface of the sand were seen atop three nests in 1974. When I brushed back a thin layer of sand, hatchlings were found in a clump just beneath the surface. A layer of sand separated them from the empty egg shells beneath. These turtles apparently were prepared for a mass emergence as occurs in *Chelonia* (Carr and Hirth, 1961).

Hatchlings emerged and left nests moving in all directions. Most nests were located on gentle slopes on open sand with the river in clear view from ground level. Nevertheless, many hatchlings moved away from the water toward permanent vegetation. Most eventually turned to water, but several did not. Some of the latter were followed up to 150 m; generally such tracks led to a desiccated hatchling that was near death.

CONCLUSIONS

The single most important factor determining success in nests in this population for 2 years was the length of time in which eggs were subjected to inundation. Eggs can withstand short periods of inundation without deleterious effects but inundation longer than 2 days in early embryonic stages significantly decreases chances of normal development. Sandbars used for egg deposition represent unstable environments with various potential hazards. Water levels may fluctuate rapidly depending on rainfall and man-controlled regulation of output from dams. Nests situated at the highest points of sandbars have the greatest chances of survival. It is adaptive to nest in permanent vegetation when water levels are high despite the increased risks. These nests are higher than any on the open sandbars; they contribute to the annual crop of hatchlings and may provide the entire crop in years when water levels remain high. Nesting success in 1973 and 1974 contrasted sharply and reflected the devastating effect of flooding in 1973. In

his demographic analysis of *Chrysemys picta*, Wilbur (1975) concluded that its life history was attuned to an extremely unpredictable chance of reproductive success, and this probably is true for *T. muticus* also.

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RELATIVE CLIMBING TENDENCIES OF GRAY (*ELAPHE OBSOLETA SPILOIDES*) AND BLACK RAT SNAKES (*E. O. OBSOLETA*)

JEROME A. JACKSON

ABSTRACT: Thirteen gray and eight black rat snakes were individually introduced into a room in which the only shelters were three wooden boxes: floor level, atop a 1-m log, and atop a 2-m log. Both races showed a statistically significant preference for the boxes atop the logs. Black rat snakes were found more frequently at floor level than were gray rat snakes, and gray rat snakes were found more frequently atop the 2-m log than were black rat snakes. The greater arboreality of gray rat snakes is interpreted in terms of the relative lack of caves and rock formations as hiding places in the Gulf states and the potential danger of fire in southern pine forests.

THE gray rat snake (*Elaphe obsoleta spiloides*) has been suggested to be the most arboreal race of its species (Curran and Kauffeld, 1937; Wright and Wright, 1957), though no quantitative evaluation of this suggestion has been made. In an earlier study (Jackson, 1974) I examined the potential predator-prey relationship existing between gray rat snakes and Red-cockaded Woodpeckers (*Dendrocopos borealis*) and hypothesized that some of the unique adaptations of this bird are related to the greater arboreality of rat snakes in the southeastern United States. I here present data to support the hypothesis that the gray rat snake is more arboreal than its

northern relative, the black rat snake (*Elaphe obsoleta obsoleta*).

MATERIALS AND METHODS

To test climbing tendencies I used 13 gray rat snakes (8 ♂♂, 5 ♀♀) captured in Oktibbeha County, Mississippi, and 8 black rat snakes (6 ♂♂, 2 ♀♀) from eastern and southeastern Oklahoma and Sumner County, Kansas. Snout-vent length of the gray rat snakes ranged from 106.6-146.1 cm (\bar{x} = 123.5 cm); that of the black rat snakes ranged from 83.2-140.3 cm (\bar{x} = 120.0 cm). All snakes had been in captivity for at least 2 months, fed a diet of