POPULATION ECOLOGY OF THE SOFTSHELL TURTLE, TRIONYX MUTICUS

by

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CONTENTS

I. INDIVIDUAL MOVEMENT PATTERNS

INTRODUCTION

Few studies have addressed a comprehensive approach to spatial organization in aquatic turtles. The more thorough treatments of this subject have been of turtles in ponds. Such studies have shown that many kinds of aquatic turtles have individual home ranges to which they will return if displaced; individuals wander extensively on land at certain seasons; also, females may make long aquatic movements associated with nesting (e.g., Cagle, 1944; Sexton, 1959; Moll and Legler, 1971). Few investigations have involved river and stream populations. Marchand (1945) indicated that populations of _Pseudemys_ may inhabit certain limited lengths of stream. Ernst (1970b) found that _Chrysemys picta_ will home to a pond via streams. Moll and Legler (1971) described home ranges and homing movements of adult _Pseudemys scripta_ in a river. If aquatic turtles exist as discrete local populations in lotic communities, then such habitats represent potentially harsh environments that might affect the integrity of turtle populations. The possibility of being displaced by water currents exists continuously, and is intensified by the scouring action of floods. Movement patterns of turtles in these situations should be described and analyzed for insight into the adaptive nature of the behavior. This paper is concerned with description of individual movement patterns in a river population of the softshell turtle, _Trionyx muticus_.

MATERIALS AND METHODS

Three methods were used in gathering data on movements: radiotelemetry, visual tracking with balloons attached to the turtle, and capture-mark-recapture.

I relied extensively on radiotelemetry. The basic radiotelemetry system used was that of Shirer and Downhower (1968) with an improved receiver. This receiver was designed for low noise, narrow band reception, and a frequency resetability of a few hundred Hz. Changes in the basic system were all associated with modifying the transmitters for use in water. The most important problem encountered was the large and increasing attenuation of signal strength as the transmitters were submerged to greater depths. In order to maximize the receiver sensitivity to weak signal strengths, a single, omnidirectional $8\frac{1}{2}$ ft. ($\frac{1}{4}$ wave) whip antenna was used. The antenna was mounted on a 14 ft. aluminum boat powered by a 20 horsepower outboard motor. This system proved to be more sensitive than a directional 30 cm loop antenna, although directional ability was lost. Since searching for transmitting individuals involved working along one axis, a river, strength of signal proved adequate for locating individuals. This technique normally permitted one to localize an individual within 20 m. By substituting a 10 cm diameter loop antenna at this point, the investigator could track a signal to its source, and physically retrieve the turtle, if it was burrowed into the substrate.

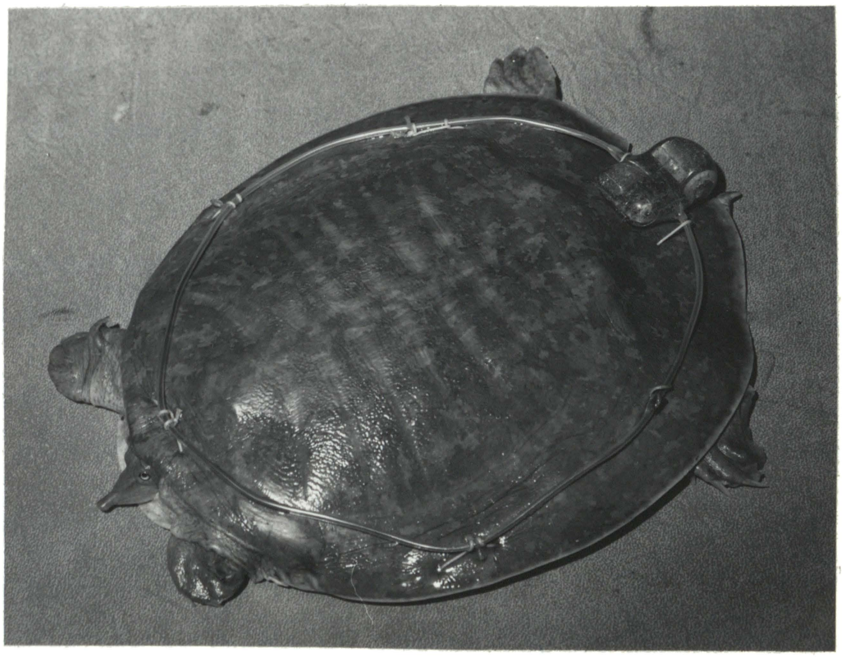
Transmitters powered by Mallory RM1RT2 mercury batteries averaged 34 days (range 22-61) battery life. The transmitting antenna consisted of a one-turn loop (117 mm diameter on males; 160 mm on females) covered with vinyl tubing. Transmitters were timed to pulse at a duty cycle of approximately 0.1 second on, 0.9 second off. There was no noticeable wandering of carrier frequency during the life of the transmitters. Transmitters (15 x 25 x 37 mm and 25 gms.) were sealed in epoxy and sewn to the edge of the turtles' carapaces with 30-lb. test braided nylon fishing line (Fig. 1). Transmitters were installed in the field on freshly caught turtles, which were subsequently released at the point of capture and allowed to burrow into the substrate.

Twenty-eight turtles (11♂♂; 17♀♀) equipped with transmitters were located 741 times over a period of 910 turtle-days in 1974. Relocations were distributed approximately equally throughout the season. After initial problems of modifying transmitters to an aquatic system were solved, only one transmitter failed to function properly in the field. Turtles normally were relocated daily -- usually at about the same time each day.

Average detection distance was 200-300 m. Maximum detection distance, 700 m, was possible only when the animal was out of the water (basking) or in shallow ($<$100 mm) water. In a deep pool, the signal would vary from extremely strong to completely undetectable within a few seconds as an individual changed depths. Individuals in 1.5 m of water could be detected at a distance of about 30 m. The signal was lost at an estimated depth of about 4-5 m when the receiver was directly above the transmitting turtle. Signal strength and the waxing and waning of signals could be used to determine the activity level of the individual and also the depth at which it was active.

Movement also was studied by attaching a small (12 x 140 mm) balloon, inflated with air at one atmosphere of pressure, to the posterior edge of the carapace by a 30 cm length of fine piano wire. By using differently colored balloons and marking them with different numbers of rings with a permanent felt-tipped marker, several turtles could be marked uniquely. Visual contact was achieved by searching through 7x binoculars. Fine, stiff wire minimized the chance of entanglement

Fig. 1. Female T. *muticus* with transmitter sewn onto the edge of her carapace at six different points.



in debris and readily pulled out of the carapace when entanglement occurred. There was no noticeable behavioral difference between turtles pulling these floats and non-tagged turtles. Tagged turtles readily submerged with the balloons and the movement data were comparable to those obtained by telemetry. Balloon tracking was especially effective for following males and immature females on sandbars where water was shallow and relatively free of debris so the balloons were continuously visible. Balloon-tracked turtles normally were relocated once per day, although many were relocated twice per day and some were tracked continuously for several hours. Balloon tagging was done in the 1972 and 1973 field seasons.

An extensive capture-mark-recapture program, begun in July 1972, yielded some information on movements. Wire mesh funnel traps were placed every 100 m along a 1.5 km length of sandbar (the main study area). Turtles also were captured by probing in shallow water along sandbars. This program was part of a larger study of population ecology which has yielded approximately 3700 captures on 2700 turtles.

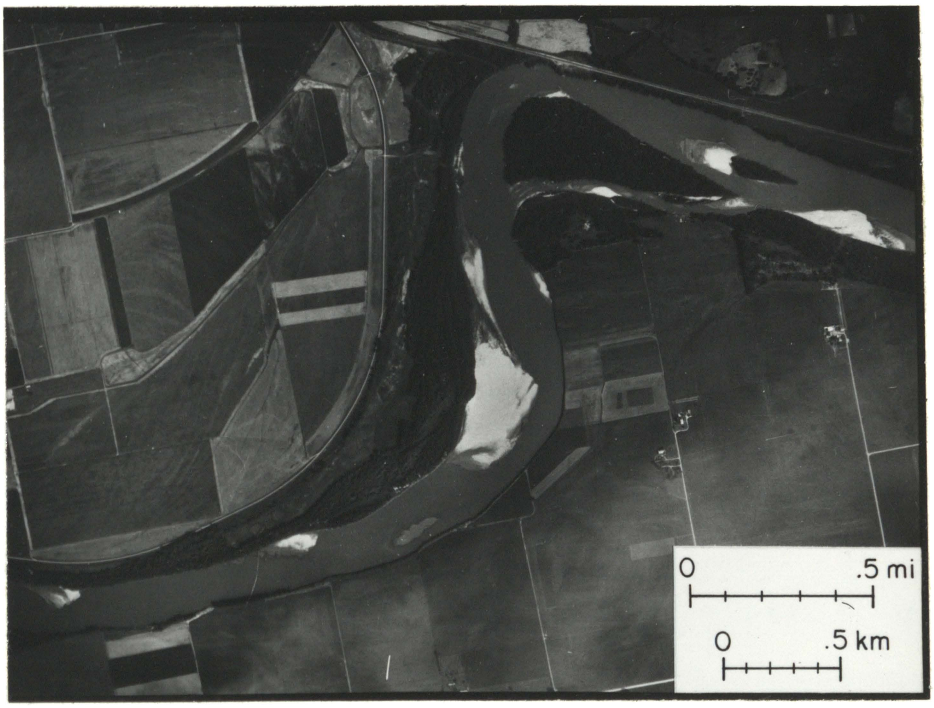
Long movements were plotted directly on an aerial photograph of the study area (Fig. 2). This area was a length of the Kansas River from the Bowersock Dam at Lawrence, Douglas County, Kansas, to 14 km downstream. Numbered stakes were placed every 100 m along the main study area (Fig. 3) so that more accurate measurement of movements could be made.

Plastral length of turtles was measured with a plastic ruler midventrally from the most anterior cartilaginous portion to the posterior edge.

Fig. 2. Aerial photograph of study area taken 5 September 1974. Current flows to the right.


0
1 mi
0
1 km

Fig. 3. Aerial photograph of the main study area taken 5 September 1974.


0
.5 mi
0
.5 km

ACTIVITY AND HABITAT

With some variation, most activity is concentrated from late April to late September. Mating takes place after emergence in the spring (Plummer, 1976), and nesting occurs from early June to mid-July (Fitch and Plummer, 1975). Nocturnal activity was not observed.

Characteristic of Great Plains streams (Metcalf, 1966), the Kansas River is subject to rapid fluctuations in water level and turbidity. In 1974, however, water levels remained low and were stable for most of the field season, with the same sandbars generally present throughout the season (Fig. 4). Water velocities in 1974 (measured with a Pigmy Current Meter, Scientific Instruments of Wisconsin, Inc.) averaged about 0.30 m/sec. near sandbars and about 0.60 m/sec. in midstream. Velocities as high as 2.1 m/sec. were measured near the dam and as low as 0.06 m/sec. on the lee side of sandbars. Average velocity of a water column is defined as that velocity measured at a point of 0.6 of the depth as one descends into the column. Velocities were taken in depths ranging from 0.6-1.2 m.

Turtles were seen in virtually every habitat in the river. Males seem to prefer the shallow water around sandbars while females seem to prefer deeper water, except in the nesting season (Plummer, 1975). Areas of activity for both sexes usually were associated with appreciable current.

HOME RANGE

Burt (1943) originally defined home range as the area in which an animal carries out its daily activities. Implicit in this definition is the dynamic nature of home range. Eisenberg (1966) stated that

Fig. 4. Habitat of T. muticus, sandbar at main study area.

social organization in mammals (including home range and other spatial relationships) is potentially the most variable factor characterizing a given species because it reflects the sum total of all the adjustments to the environment in terms of habitat exploitation and energy budget. Thus, when the environment changes, such as when new food sources become available in previously unused areas, chipmunks (Martinsen, 1968) shift their home ranges to exploit such resources. Likewise, when the physical nature of the habitat changes, as when vegetation structural types change in a pond, turtles of the genus Chrysemys shift their activity ranges (Sexton, 1959).

Softshell turtles inhabiting riverine situations are subject to extreme changes in the physical structure of their environment. Small sandbars may have a lifespan of only a few days when water levels fluctuate frequently. The contours of larger, more permanent sandbars have subtle daily changes and, on a yearly basis, changes in shape and in physical composition of the sandbars may be drastic.

For these reasons home ranges of turtles were determined on a time-qualified basis. Generally, ten consecutive days of location was considered minimal to compute a home range. Most turtles with transmitters were tracked for 34 days. However, during this time, 4 of 7 males and 3 of 9 females shifted their home ranges. Locational data for some turtles consisting of several recaptures extending over a given season were not used in computing home range size and location. Many such turtles were recaptured in areas extending 2 or 3 km. Radio-tracking revealed the nature of movements in these areas and generally conflicted with the classical concept of a home range as a well-defined area used regularly and permanently. For T. muticus, computation of a single home range based on several years of recapture data would be an exercise of dubious value.

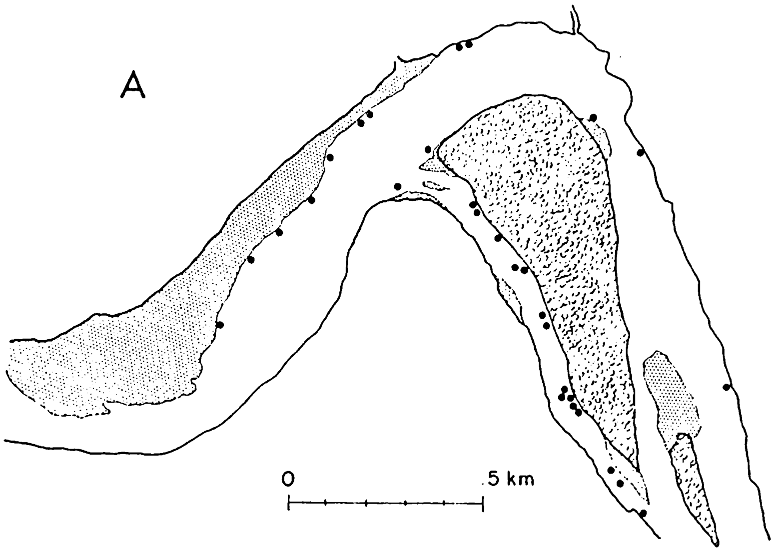
Several recent attempts to model home ranges statistically employ utilization distributions (e.g., Koeppl, et al., 1975). Locational data of T. muticus within their home ranges generally were normally distributed. However, when 95% confidence limits were applied to a given set of home range data, the home range size generally was inflated (i.e., confidence limits were greater than ranges) and included areas that individuals did not visit as shown from daily monitoring. For these reasons it seemed that a simple range of clustered locational data was more conservative and best described the individual home range size.

Most movements of softshells are aquatic. Both males and females frequently bask on sandbars and mudbanks usually within one meter of the water. Females wander as far as 90 m from the river in search of suitable nesting sites (Fitch and Plummer, 1975), but these movements are limited to sandbars. When the water level drops rapidly, burrowed turtles may be left behind on exposed sandbars but quickly make their way back to the river. Foraging behavior sometimes leads turtles onto sandbars. Tracks frequently were seen leading to dead fish as far as 10 m from water; the tracks always led directly to the fish without the random foraging movements often seen in shallow water. Unlike some aquatic turtles which seem to leave the water and spend the winter in terrestrial hibernacula (e.g., Clemmys, Netting, 1936; Kinosternon, Bennett, 1972), T. muticus appears to hibernate underwater buried in the substrate. In October when activity is rapidly waning, tracks were never observed leading away from the water. Three turtles with transmitters (1♀; 2♂♂) became inactive under about 1-1.5 m of water at that season. Turtles occasionally were located in mid-stream on small, protruding sandbars. Open water generally was avoided, but occasionally turtles crossed the river or made long movements upstream or downstream (see below). Home ranges, therefore, are linear and movements within home ranges correspond closely to the contours of the shoreline (Fig. 5). When home ranges of all individuals recorded are plotted on a common map, the pattern is a mosaic of grossly overlapping areas. No observations were made which would suggest territoriality.

Since home ranges are linear, length is the critical dimension. Home ranges were measured when an individual stayed in an area 10 or more days within the life of the transmitter. Locational points were clustered in such a manner (Fig. 5) as to make the home range obvious. There was no statistical difference in sizes of home ranges determined by telemetry and by balloon tagging. Size data were skewed to the right. Transformed data (i.e., to $\sqrt{Y+1}$) were normal. Variances were unequal between home range sizes of males, subadult females, and adult females. Therefore, for significance testing, the methods of Sokal and Rohlf (1969; p. 374) were used. Mean home range length and 95% confidence limits of males was 474 m (346-623); of subadult females, 750 m (512-1033); of adult females, 1228 m (814-1726). All sizes were significantly different from each other. Figure 6 summarizes these data.

Utilization of home range differs between the sexes in several aspects. Vagility (movement/day) within the home range is significantly greater in females. Males move an average of 61 m (46-78) per day; subadult females, 116 m (80-158); adult females, 165 m (131-204). If days of no movement are excluded, males spend a greater amount of time

Fig. 5. Locational points in home ranges of _T_. _muticus_. A. Adult female home range. The entire area is covered in several days; the turtle crossed the river frequently. B. Home ranges of three males. Note closely clustered points. These males crossed the river infrequently. Stippled areas indicate exposed sandbars.


A
0
5 km

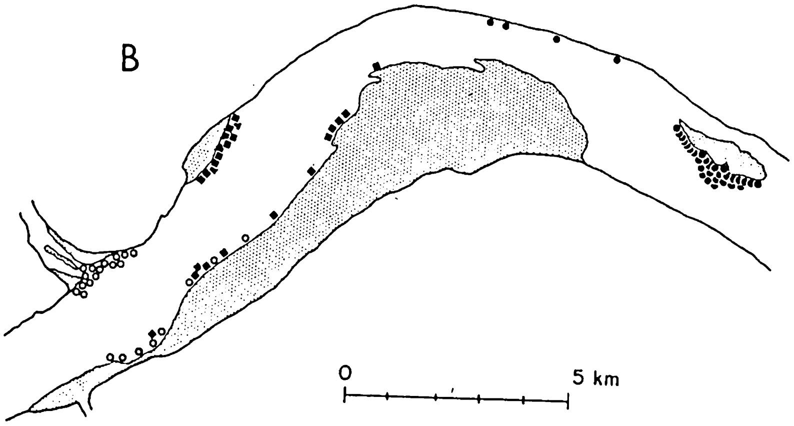
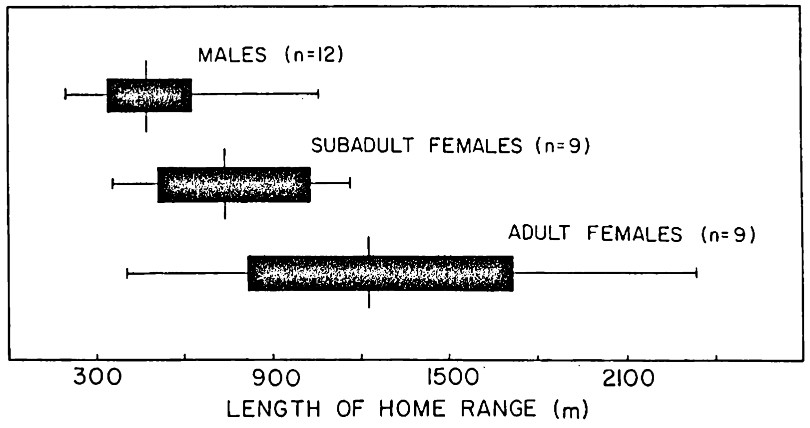

B
0
5 km

Fig. 6. Sizes of home ranges in adult males, subadult females, and adult females. Long vertical lines are means; rectangles are asymmetrical 95% confidence limits; horizontal lines are ranges. All means are significantly different from one another (♂♂ vs. adult ♀♀, $P<0.001$; ♂♂ vs. subadult ♀♀, $P<0.05$; adult ♀♀ vs. subadult ♀♀, $P<0.05$).

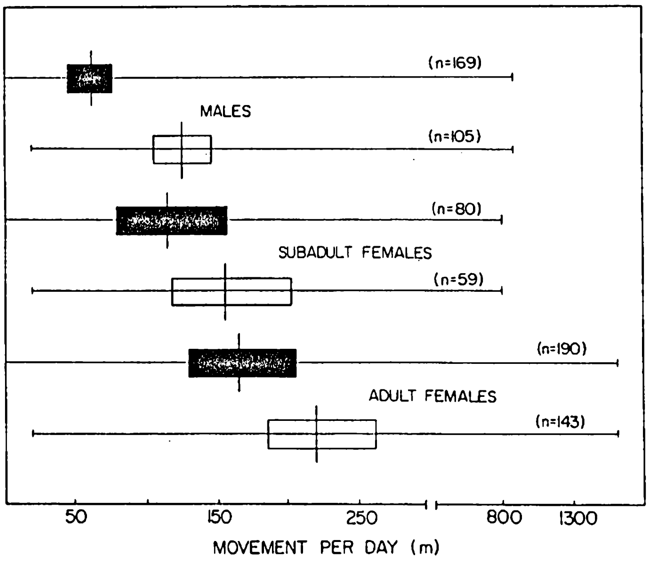

MALES (n=12)
SUBADULT FEMALES (n=9)
ADULT FEMALES (n=9)
300
900
1500
2100
LENGTH OF HOME RANGE (m)

(38% of total) in inactivity than do subadult females (26%), and adult females (25%). Although the differences in these percentages are not statistically significant, they probably are correct in indicating that females move more frequently than do males. Gibbons (1968) reported that female *Chrysemys* traveled further, more often, than did males. Ernst (1970a) found larger home ranges in female *Clemmys* than in males. Figure 7 summarizes vagility data in *T. muticus*. These data were heteroscedastic and skewed to the right, and therefore were treated in the same manner as above. It is perhaps revealing that, during floods, the only turtles that shifted appreciably and moved away from the shoreline were females.

Since most turtles were relocated only once per day, the sample values probably represent minimum estimates. Some insight may be gained by examining the data gathered from balloon-tagged turtles (4♂♂; 4♀♀) which were relocated once in the morning and once in mid-afternoon each day. If one compares the complete records of each individual with the sets of morning records, there is an increase in vagility of approximately 7% in males and 15% in subadult females. Ideally one should locate an individual many times per day for an accurate estimate of vagility. However, the difference is not sufficiently great to render the once-a-day estimates valueless. *Pseudemys scripta* in Panama returns to a home site in the evening (Moll and Legler, 1971), and if data were obtained only at this time of day, a major discrepancy would exist between the estimated vagility and true vagility. Such return to a home site was not observed in *T. muticus*.

Because females move more frequently and for longer daily distances in their home ranges than do males, it is not surprising to find that

Fig. 7. Vagility in adult males, subadult females, and adult females. Long vertical lines are means; rectangles are asymmetrical 95% confidence limits; horizontal lines are ranges. Dice grams with solid rectangles represent total vagility; dice grams with open rectangles represent total vagility minus days in which there was no recorded movement.

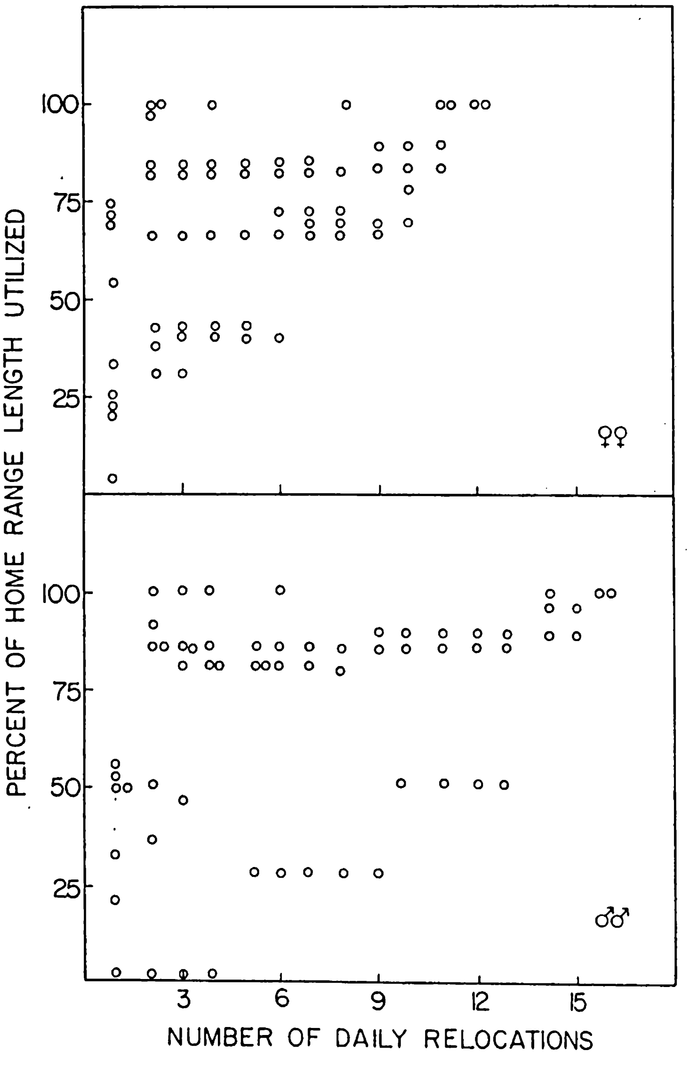

(n=169)
MALES
(n=105)
(n=80)
SUBADULT FEMALES
(n=59)
(n=190)
ADULT FEMALES
(n=143)
50
150
250
800
1300
MOVEMENT PER DAY (m)

individual females tend to occupy both sides of the river in their home ranges, whereas males tend to reside on one side. When a male did cross the river, the move was permanent, at least within the life of the transmitter. Among 179 location records of 7 males only 5% were river crossings, whereas of 85 location records of 3 subadult females 11% were crossings, and of 151 location records of 6 adult females 14% were crossings. Females cross the river more than twice as frequently as do males ($P<0.01$). The reason for this difference is uncertain but perhaps the size difference between the sexes is involved. Perhaps the larger females can better withstand the greater current velocity in open water but subadult females are approximately the same size as adult males. On those occasions when males did cross, there was no displacement downstream. Also, males appear to make long upstream movements with ease (see below).

Utilization of home range was investigated by determining the number of days elapsed while the turtle utilized 100% of the length of its home range (Fig. 8). The dependent variable was transformed to arcsin $\sqrt{Y}$, and regressed on X, the number of days. There was too much variation to show a significant regression in either case. Mean time to cover the home range was smaller in females (7.1 days) than in males (8.7 days), but this difference was not significant. The slope for females was slightly steeper than that for males. This analysis suggests that females may move though the entire home range faster than do males, but a much larger sample size would be needed to show the difference statistically. Figure 8 also indicates the need of requiring at least 10 relocations for determining home range size.

A behavioral pattern characterizing both sexes was the "escape reaction." When turtles, which are basking or are active in shallow

Fig. 8. The relationship between percent of home range utilized and time (number of days), in males and females. Females moved over area of home range somewhat faster than males; on the average however, difference is not significant.


PERCENT OF HOME RANGE LENGTH UTILIZED
100
75
50
25
♀♀
100
75
50
25
♂♂
3
6
9
12
15
NUMBER OF DAILY RELOCATIONS

water near sandbars, are alarmed, they immediately move to deep water. There they either submerge and presumably burrow into the substrate of the bottom or, less often, they swim out 15-20 m on the surface and allow themselves to be swept away by the current. This passive escape behavior normally involves drifting downstream 100-200 m, where the turtle then swims to shore. Such behavior was elicited in balloon tagged turtles when the investigator suddenly approached from a place of concealment. In several such instances the displaced turtles were seen on the following day near the points from which the escape began. The turtles captured and equipped with transmitters were released in a manner that encouraged them to burrow and remain at the capture site. Even with these precautionary measures most of the first relocations were one hundred to several hundred m downstream.

When Burt (1943) discussed the concept of home range in mammals he described temporary sojourns outside the home range area. Similar "sallies" are characteristic of _T. muticus_ (Fig. 9). These movements are characterized by brevity lasting only a few days, and in each (n=4), the sally was made upstream. There was no obvious correlation with any environmental variable. The sally made by the female in Figure 9 began on 13 July, the end of the nesting season, and conceivably could have involved search for a place to oviposit but there was no known nesting sites along the entire length of her sally.

As pointed out above, home ranges should be viewed as dynamic and subject to change in location and character. Figure 10 illustrates shifts in the home ranges of two females (both upstream). No definite case of linear shift in home range was observed in non-displaced males, but such shifts probably do occur. In the displacement experiments

Fig. 9. Temporary movements ("sallies") out of the home range. A. Female which made a 4000 m upstream sally of 7 days; downstream return movement was made in one day. Closed circles are locations recorded before the sally; open circles are locations recorded after the sally. This unusually long movement was made at the end of the nesting season and presumably could have been associated with reproduction. Similar sallies, generally shorter both in duration and distance traveled, have been observed after the nesting season. B. Male which made an upstream sally of 3 days. Closed circles are locations recorded before and after sally. Open circles are locations recorded during the sally. Directional lines do not imply path of movement in either example. Stippled areas indicate exposed sandbars.

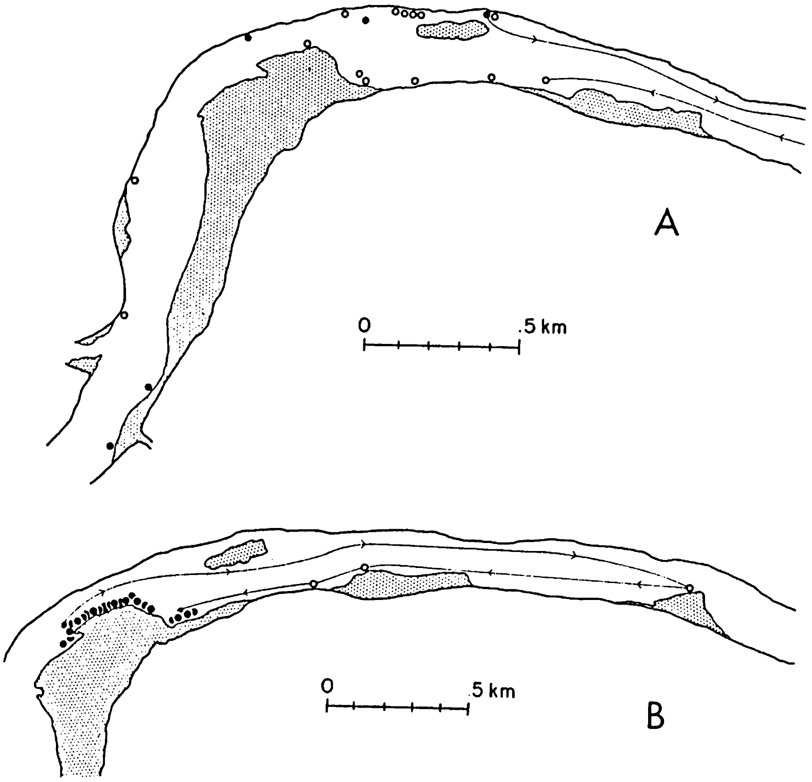
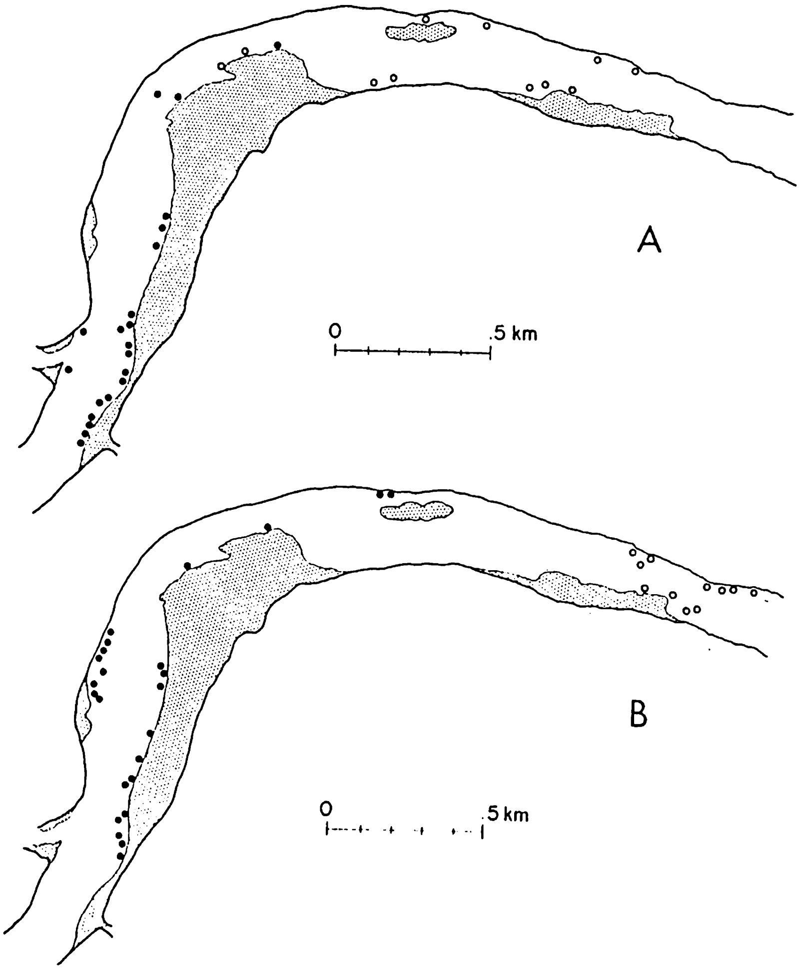

A
0
.5 km
0
.5 km
B

Fig. 10. Shifts in home range location in a subadult female and an adult female, respectively. A. Closed circles are locations recorded from 6 Jun. to 28 Jun.; open circles are locations recorded from 29 Jun. to 7 Jul. The shift represents a mean upstream movement of 1363 m. B. Closed circles are locations recorded from 23 Aug. to 15 Sep.; open circles are locations recorded from 16 Sep. to 5 Oct. The shift represents a mean upstream movement of 1534 m. Stippled areas indicate exposed sandbars.


A
0
.5 km
B
0
.5 km

described below males moved up- and downstream, establishing home ranges of varying duration. Shifting of home range location was distinct. Usually it was abrupt; a single long move in one day, served to relocate the new home range. This behavior was much like that in sallies but in the latter, the turtle returned within a short time to its home range. This similarity suggests that sallies may be exploratory movements made when for some reason, the home range becomes unsuitable.

Webb (1961) suggested that wandering might be elicited by rapid fluctuation in water level presenting different morphometric habitats to turtles and rendering it difficult for them to recognize any localized features that might serve to define a home range. Sexton (1959) found much seasonal shifting of activity ranges in Chrysemys in a small pond with unstable water levels. This contrasted with sedentary behavior of Chrysemys in a relatively more stable lake (Pearse, 1923). Such findings are consistent with Eisenberg's (1966) view that spatial organization within a species is fluid, capable of changing in different environments. The large range and variance in size of home range among softshells (Fig. 6) probably reflects this same phenomenon.

Why individual softshells shift their ranges is unknown. No obvious environmental variable could be correlated with the shifts. In each instance water levels had been stable for several weeks and there had been no noticeable change in variation in water temperature.

LONG MOVEMENTS

In June 1973 many females were tagged with balloons and released but few of them were ever seen again. It is unlikely that the balloons were immediately lost. Females have thicker, and consequently stronger carapaces than males for attachment of the wire; yet males tagged with balloons did not disappear so consistently. Females were known to resort to shallow water in large numbers in June as they were frequently trapped there. The only plausible explanation for the regular disappearance of the balloon-tagged females is that they move much further than males and consequently leave the area of capture rapidly and are soon lost in most instances. After a substantial number of balloons had been attached to females, I began to recover lost balloons which were usually entangled in overhanging vegetation at distances of one to several km up- and downstream from the release point. Consequently, balloon-tagging of adult females was abandoned in favor of radiotelemetry.

The first successful transmitters were attached to females in the spring of 1974. Movements by these females were so extensive as to preclude the monitoring of many individuals simply because it would not have been possible to find them all in one day. One female (No. 1289) moved a total of 21.8 km in 20 days (although there were 5 days when no detectable movement occurred). She ranged 4 km downstream from the release point and 6.8 km upstream, passing the release point twice. Another, subadult female (No. 1291), moved 10.5 km in 16 days (two days spent with no movement) to a distance of 6.8 km above the release point, averaging 658 m per day. Seventy-seven percent of her daily relocations were upstream from the previous day's location. Table 1 summarizes early season movement patterns of four females, two of which eventually settled into home ranges, comparable to those maintained after the nesting season.

Males also make long movements (Fig. 11); these movements could not be correlated with any specific time of the season, nor could any pattern be discerned among them.

Table 1. Summary of movement data for females in the nesting season. Vagility is much greater than that within established home ranges. All cases of extended long movements in females were in the reproductive period. Subadults also appear to make extended long movements. The values in parentheses for vagility indicate total vagility minus days of no recorded movement.

Turtle No.	Length of Plastron (mm)	Mean Vagility (m/day)	Size of home range (m)	Distance of home range from release point (m)	No. Relocations in home range	Dates of Observation
1289	147	1091 (1451)	----	----	---	3 Jun - 29 Jun
1291	111	658 (752)	----	----	---	12 Jun - 13 Jun
1258	146	1305 (1740)	900	6100	26	27 May - 6 Jul
1264	128	690 (828)	1400	4100	50	27 May - 31 Jul
TOTAL (Means)		907 (1126)	1150	5100	38	------

Fig. 11. Histogram of long movements in males and females. Both sexes appear to make long movements up- and downstream.

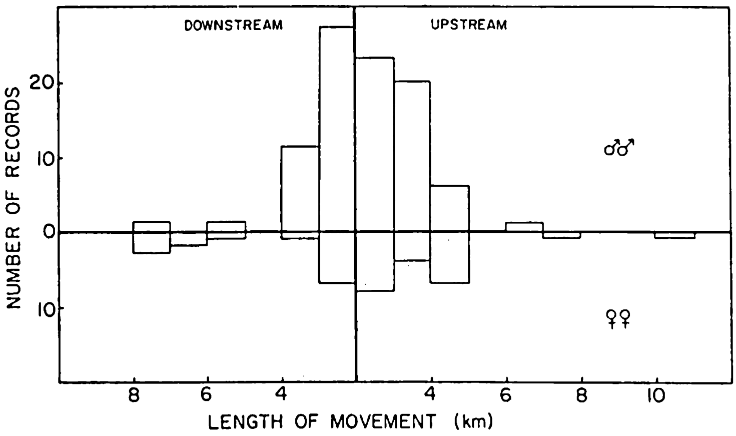

DOWNSTREAM
UPSTREAM
♂♂
♀♀
NUMBER OF RECORDS
20
10
0
10
8
6
4
4
6
8
10
LENGTH OF MOVEMENT (km)

Table 2 illustrates some selected examples of long movements and shows the times involved. From these limited data it appears that daily upstream movements of at least 3-4 km can be attained by adult females, and 2-3 km by subadult females and adult males.

Several relocations were made on turtles during long movements. Signals detected under such conditions usually were weak with sudden variations in strength, and were in the main channel removed from the shoreline. These characteristics suggest that when making long movements, turtles travel in deeper, more open water than they frequent ordinarily during a home range sojourn. In a biotelemetric study of Pseudemys, Moll and Legler (1971) found that the turtles spent little time in open water and concluded that they moved there only when traveling from one area of activity to another.

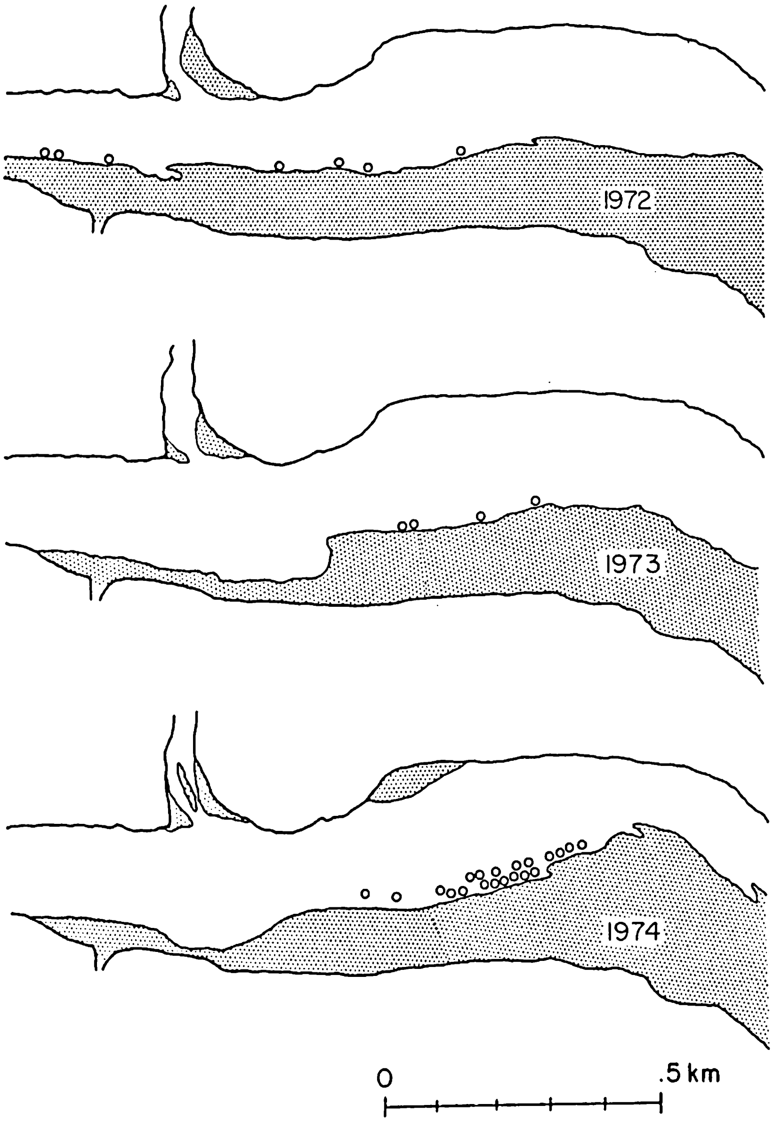
HOMING BEHAVIOR

Figure 12 shows locations of a turtle captured in three consecutive years. Fidelity to specific locations is also shown in the return to them after sallies, and return after escape reactions. However, by walking down the bank and making oneself conspicuous near an escaping turtle, one could induce the turtle to continue downstream for long distances. Tagged turtles seemed not to return immediately to their home ranges but settled, at least temporarily, in an area near where they were displaced. Such behavior prompted experiments in which turtles with attached transmitters or balloons were artificially displaced by transporting them in a closed container in a boat either upstream or downstream.

Table 2. Selected records of long movements of *Trionyx muticus*.

Turtle No.	Sex	Length of Plastron (mm)	Length of Movement (m)	Time of Movement (days)	Direction of Movement
572	♂	102	2160	3	Upstream
1215	♂	102	1980	1	Upstream
390	♂	96	3510	4	Upstream
810	♂	98	1900	2	Upstream
1462	♂	110	2900	1	Downstream
1289	♀	147	7800	2	Upstream
1473	♀	138	4100	1	Downstream
1258	♀	146	3300	1	Downstream
1291	♀	111	2100	1	Upstream
489	♀	103	2300	1	Upstream

Fig. 12. Locations recorded for the same subadult female _T. muticus_ in three consecutive years; by balloon tagging in 1972; recaptures in 1973, and radiotelemetry in 1974.


1972
1973
1974
0
.5 km

Nine turtles (4♂♂; 5♀♀) were equipped with transmitters and displaced from their capture points on the main study area. For some of the displaced turtles the home range was known; in the others the point of capture on the main study area was assumed to be within the home range. Fates of these turtles are summarized in Table 3. In addition, 21 "foreign" turtles, captured upstream or downstream from the main study area, were released on the main study area with balloons attached. Only four males (Table 4) and one female carried balloons long enough for movements to be determined.

Two males displaced upstream illustrate two basic contrasting behavioral patterns that characterized most displaced turtles. One (No. 909) displaced 3400 m upstream, spent the next 27 days in a home range which included the point of release. The other male (No. 1462), when displaced 4000 m upstream spent two days at the point of release, then moved 3000 m downstream the following day. It spent two days at this point but then moved another 2300 m downstream the following day, moving past the point of initial capture. The next 29 days were spent in two home range sojourns of 12 and 15 days, respectively, interrupted by additional downstream movements totaling 1650 m. Most of the other displaced males (transmitter-equipped and balloon-tagged) behaved similarly. Displaced males either established home ranges at the point of release or wandered extensively, upstream and downstream. Number 390 (Table 3) returned to a home range occupied in 1973 and 1974 only after a probable 850 m escape reaction which was induced by replacing the battery in its transmitter.

Displacements of females with transmitters were limited to August and September in order to avoid the long movements that occur in the

Table 3. Fate of displaced turtles equipped with transmitters. Fate is defined as the activities and location of the turtle during the last few days that the transmitter was operating. See text for details of these experiments.

Turtle No.	Sex	Length of Plastron (mm)	Length of Displacement (m)	Direction of Displacement	Period of Observation (days)	Fate
909	♂	105	3400	Upstream	27	Home range at release point
1462	♂	110	4000	Upstream	35	Home range at 2950 m downstream from point of initial capture
810	♂	98	3600	Downstream	28	Sally (?) from home range at 900 m downstream from release point
390	♂	96	2700	Downstream	63	Return to area of initial capture
1615	♀	133	2700	Upstream	39	Return to area of initial capture
1614	♀	132	2700	Upstream	39	Return to area of initial capture
489	♀	103	2400	Upstream	33	Home range at 900 m upstream from release point
1616	♀	135	4000	Downstream	41	Home range at 3100 m downstream from release point
67	♀	117	2000	Downstream	29	Home range at release point

Table 4. Fate of displaced males tagged with balloons. Each turtle was displaced approximately 2700 m upstream.

Turtle No.	Length of Plastron (mm)	Period of Observation (days)	Fate
974	102	6	Remained at release point
532	103	6	Remained at release point
865	99	7	Remained at release point; recaptured 2500 m upstream the nest year
569	92	3	Returned to area of initial capture

nesting season. Two adults displaced 2700 m upstream, were assumed to have had home ranges (based on two captures within one week) at the point of capture. Number 1615 was located within her home range the day following her displacement and 22 times more in the next 38 days. Number 1614 spent 18 days in the release area before returning to the area of initial capture where she was located for the next 21 days. Of the remaining three displaced females with transmitters (1 adult; 2 subadults), one established a home range at the release point and two wandered before establishing home ranges. One female, tagged with a balloon and displaced 2800 m upstream, was observed for seven days at the release point. She was recaptured at the point of initial capture 53 days later and again was displaced to the same release point. Here she was recaptured the following year. It appears that she homed after the first displacement but failed to do so after the second.

Behavior after displacement is similar in males and females; little homing tendency was observed. Displaced turtles exhibited confinement to home ranges, utilization of home ranges, sallies, and shifts of home ranges similar to non-displaced turtles.

DISCUSSION AND CONCLUSIONS

Based on the meager information concerning aquatic movements in Trionyx, two contrasting views may be seen. Breckenridge (1955) marked 172 Trionyx and recaptured 30 over a seven year period. The greatest distance between captures was 600 yards, suggesting that these turtles are relatively sedentary. Both Breckenridge (1955) and Webb (1962) cited cases of commercial fishermen trapping and netting in one area over an extended period with progressively fewer captures of Trionyx.

Such data tended to support the hypothesis that softshells are sedentary. On the other hand, Cahn (1937) stated that many softshells sometimes may be seen immediately below dams because they frequently travel long distances upstream, and are concentrated where their passage is blocked by the dam.

No such large concentrations were observed below the Bowersock Dam at Lawrence in this study. Population densities immediately below the dam seemed to be about the same as on certain sandbars several km downstream. Perhaps Trionyx are more easily observable below dams which might lead one to believe that they are more numerous. No massive movements were observed, although individuals did make long upstream movements.

Rapid and long movements, some against the current, existence of definitive home ranges, the return to home ranges from sallies and the subsequent shifting of home range location all demonstrate that these turtles are not totally at the mercy of the current. Softshells frequently were observed moving with ease in water flowing 2.1 m/sec. I have found that this species is highly vagile, with a distinct, significant difference in vagility between males and females.

This study also has indicated the necessity of qualifying home ranges with a time limitation. Comparison of home range parameters between sedentary and highly vagile species may be invalid unless this important concept is considered. Homing movements likewise, should be time-qualified. For example, nos. 1614 and 1615 (Table 3) were displaced upstream the same distance at the same time; no. 1615 was back in her home range on the following day but no. 1614 spent 18 days at the release point before returning. Both turtles were considered to have homed, but the nature of homing (i.e., immediately vs. delayed) was quite different even though both had the potential to return to their home range within a few hours. Greater time spans (5-763 days) between displacement and return to home range have been reported by Ernst (1970b) for Chrysemys picta. In the present study turtles were necessarily considered not to have homed if they did not return within the life of the transmitter. Obviously homing studies based on long-term observations such as capture-recapture are not directly comparable (re percentage of turtles homed) with those utilizing short-term observational methods.

The apparent lack of immediate homing responses in displaced turtles caused doubt about the fidelity of T. muticus to its home range. Most turtles established normal home ranges at locations other than their place of initial capture (Tables 3 and 4). Even turtle no. 390 would not have been considered to have homed if it were not for an escape reaction.

Turtles may at times be swept downstream by the current, but no known natural phenomena would displace them comparable distances upstream. Hence better homing performance could be predicted for animals displaced downstream than for those displaced upstream. Miller (1954) found this to be so in a homing study of cutthroat trout, Salmo clarkii; fish displaced upstream moved erratically and some individuals actually moved downstream past their home ranges. Similar behavior was observed in my study of Trionyx (No. 1462, Table 3). Moll and Legler (1971) tagged seven Pseudemys with biotelemetric devices and displaced them for various distances up- and downstream. All three individuals that were displaced upstream, homed. On the other hand, Ernst (1970b) released 50 Chrysemys one mile upstream and 50 one mile downstream from their home pond, and found that 25 of the upstream-displaced individuals eventually returned whereas only 22 of the downstream-displaced individuals returned. Only 12 of 60 turtles displaced two miles downstream returned. In my study two of the three Trionyx with transmitters that homed were displaced upstream; these results do not support the hypothesis of differential homing ability based on direction of displacement. No balloon-tagged turtles were displaced downstream but one male and one female homed after upstream displacement.

There remains an alternate explanation for the results of the homing experiments with Trionyx. Because home range shifts are common and because turtles appear to make long movements from time to time, the entire area of my study may be familiar to turtles. It has been stated above that individuals have much larger areas of activity for a given season or for a number of seasons than in single home ranges. Individuals often ranged several km over a given season. Displacements for the distances used in this study simply may not have stimulated strong homing behavior. However, Breckenridge (1955) recaptured a T. ferox (=spiniferus) within 30 yards of its release point after the turtle had been displaced 30 miles three months previous. In my study the frequency with which the sampled turtles shifted their home range locations together with the above homing data suggests that T. muticus does not show a high degree of fidelity to a home range.

Other questions relevant to the analysis of spatial organization in this species are whether nesting females nest at the same location each year and whether they return to their home ranges after nesting. Gibbons (1968) suggested that Chrysemys females change locations in successive summers because of failure to return to home ranges after leaving to nest. Ernst (1970a) found that home ranges of Clemmys did not include suitable nesting sites and the females had to leave their home ranges to lay their eggs. Moll and Legler (1971) found only two major nesting areas for Pseudemys along a 7000 m length of river, and assumed that a female living within that section would move to one or the other -- a maximum of 3500 m, to nest. Three females marked on one nesting site were later relccated 300, 540, and 800 m away, respectively.

The long aquatic movements of female Trionyx in the nesting season presumably are made to reach suitable nesting locations. There were four major nesting sites included in the study area, one centrally located (the main study area), the second 2 km downstream, the third 5 km downstream, and the fourth 6 km downstream (see Fig. 2). Gravid females consequently would be within 6 km of suitable nesting sites. The data on movement summarized in Table 1 show that these females do not simply move to the nearest nesting site in order to nest. The two females tagged with transmitters which wandered and then settled in home ranges did so near the most heavily used nesting site. Both were first captured on the main study area 6 km upstream. Three of 14 females captured in 1974 ovipositing on the largest site also were originally marked on the main study area, 6 km upstream.

In general it may be concluded that individuals seem not to confine their activities to small areas over long periods and females ordinarily do not return to a specific home range after nesting.

Furthermore, the above individual movement patterns suggest that T. muticus does not exist in discrete, localized populations. Contrary to the observations made by commercial fishermen as cited above, analysis of recapture data from the main study area does not support the hypothesis that continued trapping in one area leads to increasingly diminishing returns (Plummer, 1975). This analysis also suggests wide-ranging populations. Brussard and Ehrlich (1970) emphasize that the delimitation of those aggregates of individuals (i.e., populations) which function as genetic and dynamic units should be one of the primary goals in field studies of population biology. Further studies of population structure in T. muticus, including populational aspects of movement patterns, will be reported elsewhere.

SUMMARY

Individual movements were studied in a river population of Trionyx muticus using three methods: radiotelemetry, trailing devices, and capture-mark-recapture.

Turtles are most active from late April to late September. Males exhibit home ranges throughout the season. During the nesting season, females make extended long movements out of their home ranges. Home ranges are linear and are limited by the absolute barriers of the shoreline. Female home ranges tend to be larger and include both sides of the river whereas male home ranges are smaller and are confined to one side. Within their home ranges females are significantly more vagile than males. Both sexes make long but brief movements out of their home ranges and may shift home range location during a given season. Homing experiments demonstrate that although some individuals do home immediately, most displacement is followed by extensive wandering or by establishment of home ranges at or near the point of release. Long movements, both up- and downstream, were recorded for both sexes.

Trionyx muticus is well-adapted to lotic habitats. Adult turtles may take advantage of currents in passive movement, but they are largely free of unwanted displacement and appear to move frequently and easily against the current. Such patterns have implications on the population structure of this species in lotic habitats.

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II. ACTIVITY, HABITAT, AND POPULATION STRUCTURE

INTRODUCTION

Freshwater turtles are well adapted for studies of population ecology because they are long lived, they breed seasonally, many retain records of growth in shell annuli, and individuals are easily captured and marked. Also, freshwater turtles often occur in discrete populations in partly isolated bodies of water (Cagle, 1944; Sexton, 1959; Gibbons, 1968; Wilbur, 1975), allowing relatively easy access by the investigator in capturing and marking a large segment of the population. Studies such as those of Cagle (1944), Sexton (1959), Emlen (1969), and Ernst (1971) demonstrate that individuals return to a body of water when displaced either artificially or when temporarily forced to emigrate because of adverse conditions. Discrete populations that have been studied in detail have been in lakes, ponds, or similar bodies of water with well defined boundaries. Few population studies have been made in streams and rivers. Marchand (1945) gained the impression from movement patterns of a few individuals that populations of Pseudemys occupied well defined segments of streams. Mahmoud (1969) studied individual movements and population attributes of three species of kinosternid turtles in streams. Moll and Legler (1971) found that some adult Pseudemys returned to the same general location of river after being displaced from it, but most adults marked by them were never recaptured or seen again. Bury (1975) described individual movements of Clemmys in a stream community. Plummer and Shirer (1975) demonstrated that in river populations of Trionyx muticus, individuals had restricted home ranges, but these areas of activity might be shifted frequently, and there was little tendency for the turtles to return to them after being artificially displaced. Plummer and

Shirer were convinced that the far-ranging movement patterns of individuals indicated a wide-ranging, ill-defined population with free movement throughout a large area. These findings were at variance with the generally accepted view of turtles showing high fidelity to a restricted area (Porter, 1972).

This paper presents the results of an extensive capture-mark-recapture program on a population of T. muticus inhabiting the Kansas River downstream from the Bowersock Dam at Lawrence, Douglas County, Kansas. Approximately 3700 captures of 2700 turtles were made from July 1972 to May 1975 in a 14 km section of river.

Although T. muticus is widespread occurring typically in large rivers of the central United States (Ernst and Barbour, 1972), its ecology, like that of other trionychids, remains poorly known. The population upon which this report is based has been studied in detail. Webb (1962) listed stomach contents of several individuals. Fitch and Plummer (1975) presented a preliminary report on some aspects of population ecology. Plummer and Shirer (1975), and Plummer (1975a,b; 1976) reported on movement patterns, reproduction and growth, nesting success, and courtship and mating, respectively.

METHODS AND MATERIALS

Turtles were collected in traps and by hand. Various types of traps were tested in 1972. Those that were most successful were constructed of 1-inch mesh chicken wire, measured about 20 x 50 x 60 cm and had a single funnel opening of approximately 2 x 50 cm; these traps were used exclusively after 1972. Success at trapping required that traps be set in relatively shallow water (<30 cm) and that bait be changed frequently. Traps were baited with fresh chopped fish or commercial dog food (Friskies Sauce Cubes) with equal success. Unbaited traps, or those having bait more than 1-2 days old, generally were unsuccessful. Traps were checked and rebaited daily from about May to September and about every other day earlier or later in the season. Turtles were captured by hand after locating them beneath the sand by probing with a blunt metal rod. This technique was effective when water was clear revealing disturbances in the sand where turtles had burrowed or had extended their heads to breathe. Probing was effective only along edges of emergent sandbars and was productive primarily in 1974 when continuous low and stable water levels produced relatively clear water.

Each turtle was measured, weighed, and uniquely marked with a series of triangular notches cut with a penknife at different positions into the edge of the carapace. New tissue filled the notches in about a year leaving distinct whitish scars.

The main study area was a 1.5 km section of river in which traps were set every 100 m. Additional collecting was done at locations extending approximately 6 km up- and downstream from the main study area. A water level gauge and a Taylor maximum-minimum thermometer were installed in the river 2 km upstream from the main study area and daily readings were obtained from each. Daily turbidity readings were obtained with a Secchi disk in 1974.

Width of tracks of turtles on the beach were measured between lines connecting the outermost claw marks on each side. Sizes of turtles are expressed as length of plastron (PL).

RESULTS AND DISCUSSION

Study area. - The main study area contained a sandbar that extended for its entire 1.5 km length when water level was low and was ordinarily well separated from other sandbars. It was the most extensive high sandbar along the 14 km section of river, and was the last to be completely inundated when floods occurred. It was better habitat with greater concentrations of turtles than areas adjoining it upstream and downstream. Because most previous studies of freshwater turtles have indicated that individuals are highly localized and that populations were well-defined, I assumed at the onset that the turtles of the main study area could be treated as a discrete population with emigration and immigration constituting relatively minor factors in its dynamics. However, as the study progressed, my assumption was suspect, especially after telemetric work in 1974 showed that marked turtles frequently left the main study area. Effort at collecting at locations up- and downstream from the main study area was increased during the latter part of 1974 and in 1975.

Characteristics of the Kansas River, both within the main study area and farther upstream and downstream are important for an understanding of the turtles' population structure. Within this section the river at highwater stage varied from about 150-450 m in width and in its lowest stages from about 80-250 m. Major movements of turtles were essentially linear, along the stream course. Downstream there was no obstacle to travel, and no important habitat change, but the Bowersock Dam, some 6 km upstream from the main study area, constituted an effective barrier to travel in that direction. Marked turtles traveling upstream were stopped or turned back by this barrier and hence were more likely to be recaptured than were individuals moving downstream. However, the dam did not prevent downstream movements, and the population of the main study area was diluted by immigrants entering from both ends. Approximately 2300 captures of 1500 turtles were made on the main study area. Aerial photographs and/or habitat photographs of these areas are presented in Plummer and Shirer (1975) and in Fitch and Plummer (1975), respectively.

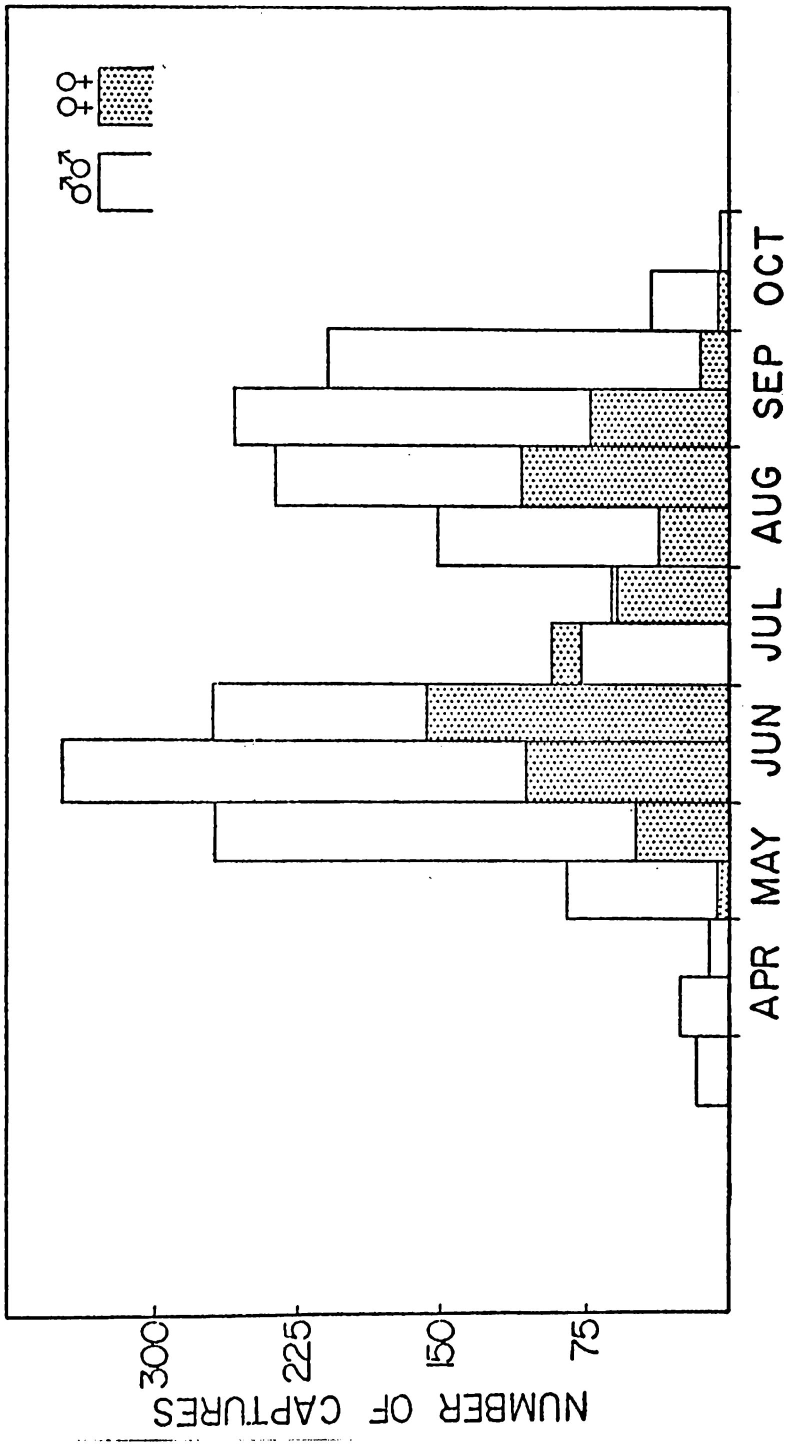
Activity. - Turtles were observed from late March to late October. Activity toward the beginning and end of the season was sporadic and strongly weather-dependent. Early and late records as well as sustained activity for different years varied several weeks (Table 1). Activity began relatively early in the 1974 season when extended warm, clear weather caused water temperatures to rise. However, sustained activity did not begin until late April when water temperatures reached 18-19°. Seventeen turtles were captured on 30 March but only four more were captured during the next three weeks. Likewise, sustained activity in the fall ceases sooner than the extreme records indicate. The season of sustained activity for most of the population is estimated at approximately five months, extending from May through September. Figure 1 shows the frequency distribution of captures for two field seasons. The distribution is bimodal with a distinct decrease in number of captures during mid-summer. Most captures during the spring peak were made with traps, whereas many of the captures during the late summer peak were made by hand. In a review of the literature on seasonal occurrence in T. spiniferus at latitudes between 40-43° N, Webb (1962) concluded that the normal period of activity is about five months, from April into September, and is dependent upon the weather.

Table 1. Records of earliest and latest dates for activity in *T. muticus* as determined by three different methods. Sign includes fresh tracks or sight records. Numbers in parentheses after each date are water temperatures of the main stream (°C).

		1972	1973	1974	1975
Spring	Sign	- - -	21 Apr. (15.0)	30 Mar. (13.5)	26 Apr. (22.0)*
	Hand	- - -	29 Apr. (17.0)	30 Mar. (13.5)	- - -
	Trap	- - -	29 Apr. (17.0)	30 Apr. (18.0)	29 Apr. (19.5)
Fall	Sign	14 Oct. (19.0)	22 Oct. (19.5)	26 Oct. (20.0)	- - -
	Hand	14 Oct. (19.0)	22 Oct. (19.5)	10 Oct. (18.0)	- - -
	Trap	24 Sep. (23.8)	10 Oct. (22.5)	21 Sep. (21.5)	- - -

*First day in field

Fig. 1. Seasonal distribution of captures for 1973-1974.

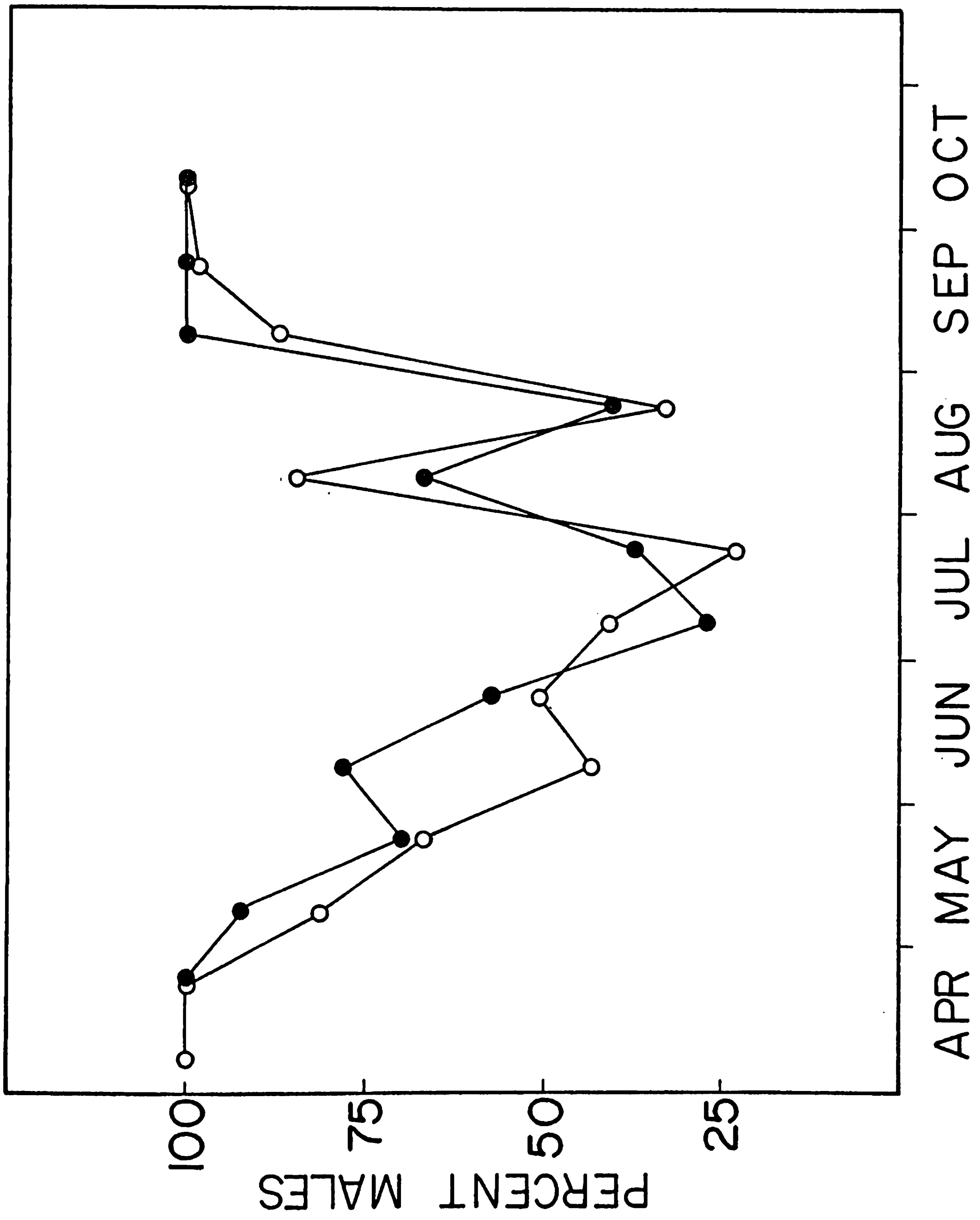

♂♂
♀♀
APR
MAY
JUN
JUL
AUG
SEP
OCT
NUMBER OF CAPTURES
300
225
150
75

In each year trap captures began later in spring and ended earlier in fall than captures made by hand and observation of sign. This disparity suggests that various types of activity occur before feeding begins early in the season and after feeding ends late in the season. Turtles would not be readily lured into baited traps unless they were feeding. However, one of two males captured on 30 March 1974 had fresh food in its stomach, and all three males captured on 9 April 1974 likewise contained food. Four of five males collected in late September 1973 contained food but two others captured on 7 October and two captured on 22 October 1973 had empty stomachs. Perhaps a tendency to bask rather than forage prevents turtles from entering traps at these times even though they are ready to feed if given the opportunity. Turtles emerge in spring at water temperatures of about 15-16° but retire in the fall at about 19-20° (Table 1). Possibly the emergence temperature is lower than temperatures at which they retire in the fall because of acclimation to warm summer temperatures.

Most of these records were those of males, and no differences among size classes in time of their spring emergence or fall disappearance could be discerned. Probably similar patterns apply to females, but fewer of them were captured. In late September two of four females had food in their stomachs. However, in spring females appeared later in samples than did males (Fig. 1), and adults appeared later than sub-adults. Only eight adult females were captured before June in three seasons of intensive collecting. However, adults occasionally were seen courting and basking.

Bias in sex ratio in samples is independent of collecting technique (Fig. 2). Ratios from each method deviate from each other only

Fig. 2. The relationship of sex ratio in samples to time of season in 1974. Closed circles are turtles captured in traps; open circles are turtles that were hand collected.

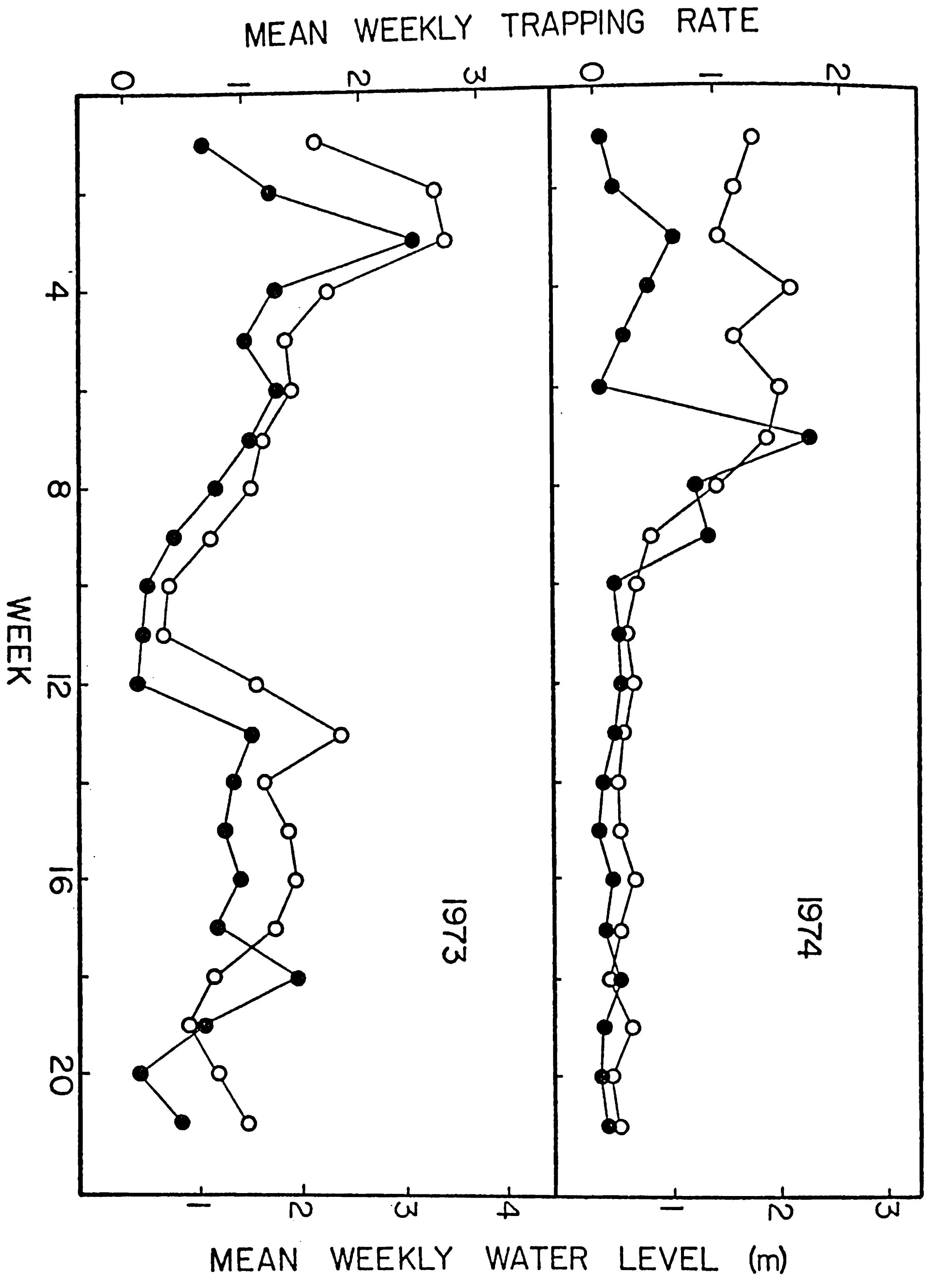

PERCENT MALES
100
75
50
25
APR
MAY
JUN
JUL
AUG
SEP
OCT

in May and early June when females are captured on sandbars in search of nesting sites, and when males are attracted to females in traps. Unbaited traps containing females attracted large numbers of males. On 10 May 1975, 36 males were found in one trap with one adult and one subadult female. Catches of 5-15 turtles in a single trap were not uncommon in spring.

Because effort in hand collecting was highly variable whereas trapping effort was approximately constant for most of the season, factors which might affect activity levels were investigated in 1973 and 1974 using trapping rates as a measure of activity (Fig. 3). In 1973 abundant rainfall throughout the year caused high and fluctuating water levels, whereas little precipitation and low, stable water levels characterized 1974. In 1973 rates were bimodal and similar to distribution of captures (Fig.1). Many turtles marked in spring were not recaptured until late summer or the following spring. In 1974 rates were unimodal with a peak in mid-June. Some turtles marked in spring were recaptured by hand in late summer and fall. Trapping rate shows a remarkable correlation with water level, usually increaing following a rise in level and decreasing following a drop. The association is extremely close in 1973 except for week 18 where the pattern is reversed. In 1974 the association is extremely close after week 7. The sharp increase in rate after week 6 followed the greatest daily increase in water level of the year from 1.9 to 4 m. Because this increase came and subsided quickly, it is not reflected as a large increase in the weekly mean.

Differences in water level *per se* probably do not affect the number of turtles entering traps. However, low, stable water levels are associated with higher water temperatures, lower current velocities,

Fig. 3. The relationship of trapping rate (no. turtles/trap-day) to water level from May-September during two years. Closed circles are trapping rates; open circles are water levels.


MEAN WEEKLY TRAPPING RATE
0
1
2
3
0
1
2
WEEK
4
8
12
16
20
1973
1974
1
2
3
4
1
2
3
MEAN WEEKLY WATER LEVEL (m)

lower turbidity, and algal blooms. High water and fast current undoubtedly scour the bottom and reduce food availability. In 1973 range of water levels was about 9 m. Perhaps baited traps are especially attractive when other food sources are unavailable during high water, or perhaps the swift current disperses the scent of bait more widely and rapidly, thus attracting more turtles. Webb (1962) mentioned that a commercial fisherman in Mississippi captured numerous softshells in unbaited traps when the river was receding from heavy rains. My general impression was that there was less activity in 1974 than in 1973, as trapping rates were lower, and sight records were less frequent. However, population estimates for the two years were similar and I found higher growth rates in 1974 (Plummer, 1975a), so perhaps activity was not greatly reduced. Turtles tagged with radio transmitters (Plummer and Shirer, 1975) did not show differences in activity levels with change in water levels, except that males tended not to move so far away from the shoreline during periods of extremely high water.

It is questionable as just how precisely trapping rates reflect activity levels as physiological, behavioral and environmental factors all affect the number of turtles entering traps (Plummer, In Press). Softshells were definitely less conspicuous during mid-summer low water periods. Trapping returns remained low during late summer in 1974, although large numbers of turtles were captured by hand in certain microhabitats.

Habitat. - Webb (1962) summarized habitat requirements of North American softshells. T. muticus seems to be more limited to large streams and rivers than the other species. The Kansas River is excellent habitat for softshells as extensive sandbars provide abundant basking and nesting sites. High population densities reflect suitability of the habitat.

There are several habitat types available to turtles within the river, including emergent sandbars surrounded by shallow water, steep mud banks shelving off into deeper water, and deep pools and channels.

Hatchlings prefer small, shallow puddles created by the highly dissected shoreline of sandbars, or the quiet, shallow waters on the lee end of sandbars. Such microhabitats contain warmer and quieter water than surrounding areas. Hatchlings burrow into the sand (silt on lee ends of sandbars) at the water's edge and were easily collected by raking through the substrate with a garden rake.

Plummer and Shirer (1975) relocated 28 T. muticus tagged with radio transmitters 741 times. Habitat at each of these relocations was categorized and all were tallied for comparison (Table 2). It was shown that males spend more time in habitats associated with emergent sandbars than do females ($t = 6.15$; $P < 0.001$). These data agree with daily observations as females were not often captured on sandbars except during the nesting season. Although males were seen in virtually every habitat in the river, they were seen in greatest numbers associated with sandbars. Basking females were not observed so frequently as males and most of them were on steep mud banks near the water. The signals of radio-tagged females frequently were lost in deep water in mid-stream, whereas those of males were almost always audible because they stayed in shallower water. Subadult females appear to be less inclined to frequent deep water than adult females, but more inclined to such habits than are males. Recapture rates of subadult females on sandbars were higher than in adults and Plummer and Shirer found that subadult females could be followed near sandbars by tagging with balloons -- a technique totally unsuccessful with adults. Females move further and more frequently than do males (Plummer and Shirer, 1975), therefore the trends

Table 2. Percent of observations of turtles equipped with radio transmitters taken in emergent sandbar habitat.

Category	Percent
Adult females	
- within nesting season	52 (112 obs. on 4 turtles)
- out of nesting season	9 (68 obs. on 2 turtles)
Subadult females	68 (270 obs. on 10 turtles)
All females	56 (450 obs. on 16 turtles)
All males	84 (287 obs. on 10 turtles)

in Table 2 may be biased because all turtles tagged with transmitters were captured and released on sandbars. However, the same trends were shown by displaced turtles which wandered extensively.

Females frequently were encrusted with epizoic colonial protozoa (primarily undescribed forms of Anarma, Epistylis, Opercularia, Rhabdostyla, and Tokophrya; Bovee, 1974), whereas males seldom had such symbionts. The colonies occurred primarily on the dorsal and ventral aspects of the posterior carapace; perhaps protozoa are worn off the anterior portions by burrowing activities. Most females had at least light growths but some individuals were heavily encrusted with thick, feathery colonies. The latter occurred primarily in early spring and early fall. The difference in occurrence of epizoics between the sexes suggests different ambient environments, males living in warmer, shallower water and basking frequently, and females living in deeper, cooler water, and basking less. Attempts at trapping in deep water were notably unsuccessful.

Sandbars contain several microhabitats, some of which are utilized by turtles more than others. Sandbars generally are molded by currents into broad flats sloping gently up to a high ridge, sloping down abruptly to a lower level which then gently slopes up to another high ridge. The resultant ridge or series of ridges, separated by one hundred to several hundred meters, are positioned at an angle to the permanent shoreline. The areas at which these ridges slope into the water are distinct microhabitats; they usually extend far out into the river, and abruptly slope into deep water at the lee edge. Frequently there are small inlets of quiet shallow water which are utilized heavily by turtles for aquatic basking late in the season. On 26 September 1974, in one such area measuring approximately 4 x 12 m, 69 males and 4 sub-adult females were captured by hand in about 30 minutes. On another occasion, in an area approximately 1.5 x 10 m on a sandbar only about 35 m in length and 1.5 km distant from the next nearest sandbar, 42 males and 6 sub-adult females were captured on one day, and 29 males, 27 sub-adult females, and 8 adult females were captured on the succeeding day. Only two males of the 64 turtles were captures from the preceeding day. Water temperature of this area was 25.5° C whereas temperature of the main stream was 19° C. All females were heavily encrusted with epizoic protozoans. Probably turtles normally staying in deeper water in preparation for hibernation, seek microhabitats which will allow them to raise their body temperature on warm, sunny fall days. Turtles rarely bask on shore during these seasonal extremes and these favorable areas along sandbars are quickly and easily accessible from deep water. Trapping returns at these times in such areas were extremely low. During most of the season turtles are more dispersed but clumping is still evident at these points, especially in terrestrial basking activity.

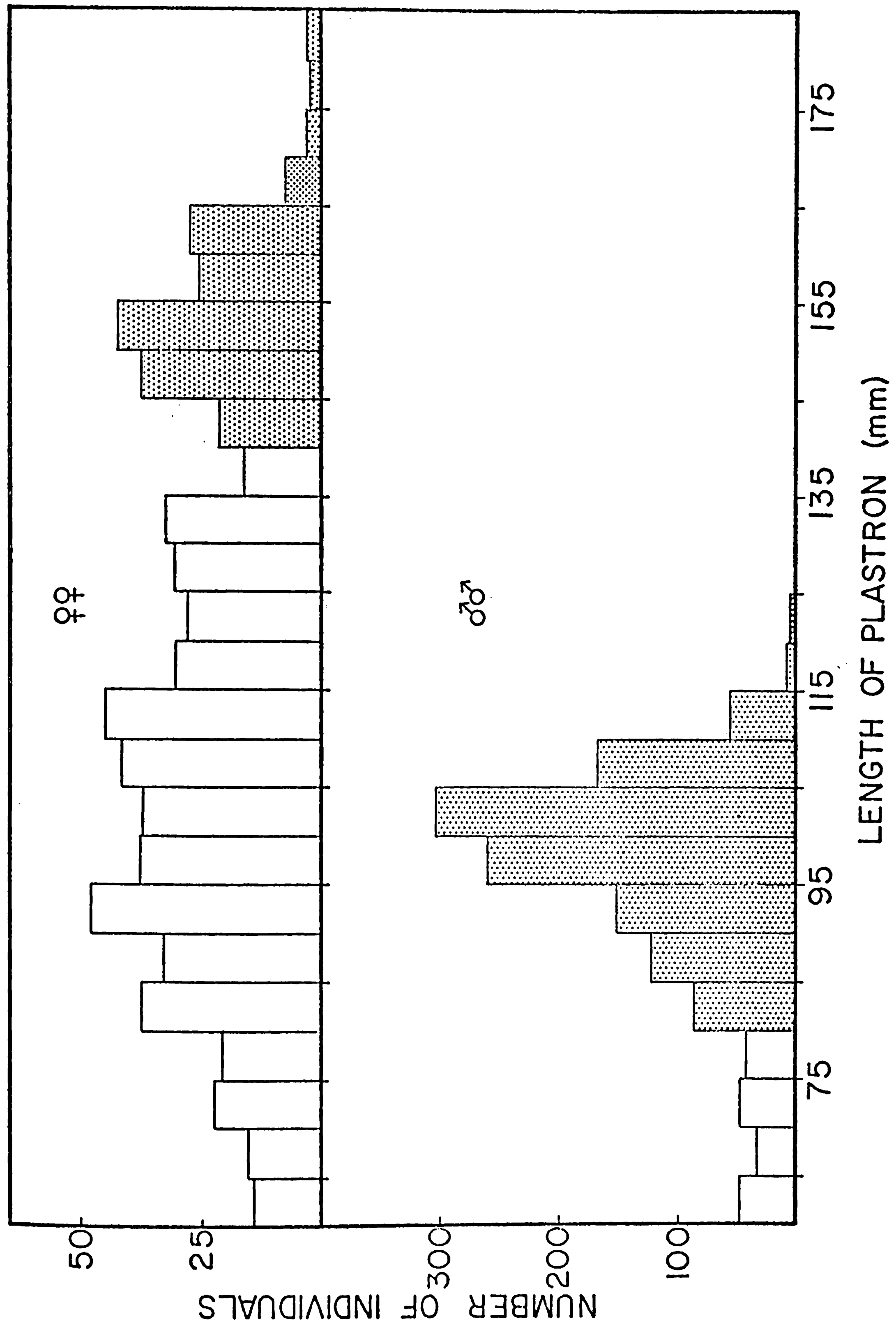
Sex ratio and size structure. - Sex ratios of juvenile turtles are generally about equal but those of adults tend to deviate from parity with females often predominating (Carr, 1952; Porter, 1972). Gibbons (1970) summarized the published information on this subject and concluded that data were insufficient to demonstrate that turtles have unequal sex ratios. Gibbons concluded that biases introduced by errors in sexing or by selective sampling caused by behavioral differences between the sexes, were present in most studies.

Male T. muticus mature at a plastral length of about 80 mm and females mature at about 140 mm (Plummer, 1975a). The largest male was 121 mm long; thus adult males and adult females fall into discrete size groups. The cloaca lies far anterior to the posterior edge of the carapace in sub-adult females the size of adult males which have the cloaca lying at or beyond the edge (Plummer, 1975a). These and other distinct secondary sexual characteristics make errors in sexing turtles highly improbable. I recorded 1162 males and 172 females, yielding an adult sex ratio of 6.8:1. The reason for this imbalance is not entirely clear, but sampling was most successful along sandbars in habitat preferred by males and was unsuccessful in deeper water where females prefer to stay. The attraction of males into traps containing females also influences the ratio to favor males. Another possible cause of male predominance could be that males mature about five years earlier than do females (Plummer, 1975a); this would be important in biasing the sex ratio of adults in a young population. Also, the sex ratio in a cohort of turtles with equal numbers of males and females would skew toward males if juveniles suffered higher mortality than adults because of the longer time that females would be exposed to the higher mortality rate. Although females move more often and farther than do males, and frequent sandbars for nesting, there is no reason to believe that mortality is higher in females. Only 15 males and 6 females were found dead during the course of my study. The causes of death in these animals were unknown. Fishermen catch many softshells on their lines and especially in their nets. During harsh winters softshells are at the mercy of large moving ice packs as they scour the bottom where turtles hibernate, but these sources of mortality probably are not sex-selective. The sex ratio of all turtles 60 mm or larger was 1.98♂♂:1♀. However, this ratio varies seasonally (Fig. 2).

Movement of females into shallow waters along sandbars during the nesting season and afterwards renders them more susceptible to capture. In four samples of softshells at various localities, Webb (1962) found 17 of 19, 15 of 15, 11 of 13, and 19 of 39 to be males. Webb believed that females occurred in shallow water where they were susceptible to trapping only for a short period before deposition of eggs. Moll and Legler (1971) likewise found pronounced seasonal changes in sex ratio in a population of Pseudemys.

Growth in males decreases abruptly after maturity and becomes asymtotic in old adults. Females mature during their ninth year and continue to grow at a reduced rate (Plummer, 1975a). The different developmental periods required for attainment of sexual maturity and the different growth rates of the sexes after maturity cause differences between the sexes in size structure of the populaion (Fig. 4). Eighty-seven percent of the males were mature, but only 25% of the females were mature. Besides hatchlings, 86 turtles smaller than 60 mm were captured, of which 13 were thought to be females and 73 males. Hence in my combined samples 82% of all males and 25% of all females were mature. Breckenridge (1955) indicated a size distribution of the sexes in a population on T. spiniferus, similar to that which I found in T. muticus. Thirty-seven percent of the T. muticus sample was immature. In studies summarized by Moll and Legler (1971) trendswere similar and they also found 37% of the population to be immature in a study of Pseudemys. However, they judged this figure to be erroneously high biased by the inaccessability of mature turtles in the river. Perhaps my estimate of the proportion of immatures

Fig. 4. Distribution of sizes for captured turtles. Stippled bars represent mature turtles.


♀♀
♂♂
50
25
300
200
100
NUMBER OF INDIVIDUALS
75
95
115
135
155
175
LENGTH OF PLASTRON (mm)

is too high because adult females were not captured in numbers representative of their true abundance.

A close relationship exists between width of track and length of plastron (Fig. 5). Each track was measured in moist sand near the water's edge. Although there is some variation in track-width depending upon individual morphometrics, speed of travel, nature of substrate, and other factors, a significant regression exists which may be used to predict size structure of the population from tracks measured on the beach. Figure 6 compares size structure of the population determined from captures to that determined from beach tracks (excluding hatchlings). Two major differences between the distributions are evident. In A, the 40-50 mm class is relatively larger; turtles of this size did not enter traps as readily as did larger turtles possibly because they occupy shallower waters than that where traps were located. The probability of locating smaller turtles by probing also was lower because of the smaller target area. The true size structure of the population probably includes a larger proportion of small turtles than capture records indicate. In B, the proportion of turtles 90-110 mm was much larger, and this probably is a more accurate representation of size structure. Basking activity is usually extremely concentrated at certain preferred sites, and mature males are most common at these sites judging from study of basking groups through binoculars. Because of the concentrated aggregations, the number of individuals represented by tracks at any given site was difficult to determine. Generally there was a mass of interconnecting tracks greatly obscured where turtles had pivoted on their plastrons orienting to the sun.

Fig. 5. The relationship of width of track to length of plastron in 73 turtles. The regression equation is $\overline{Y} = 11.78 + 0.93x$ ($P < 0.001$).

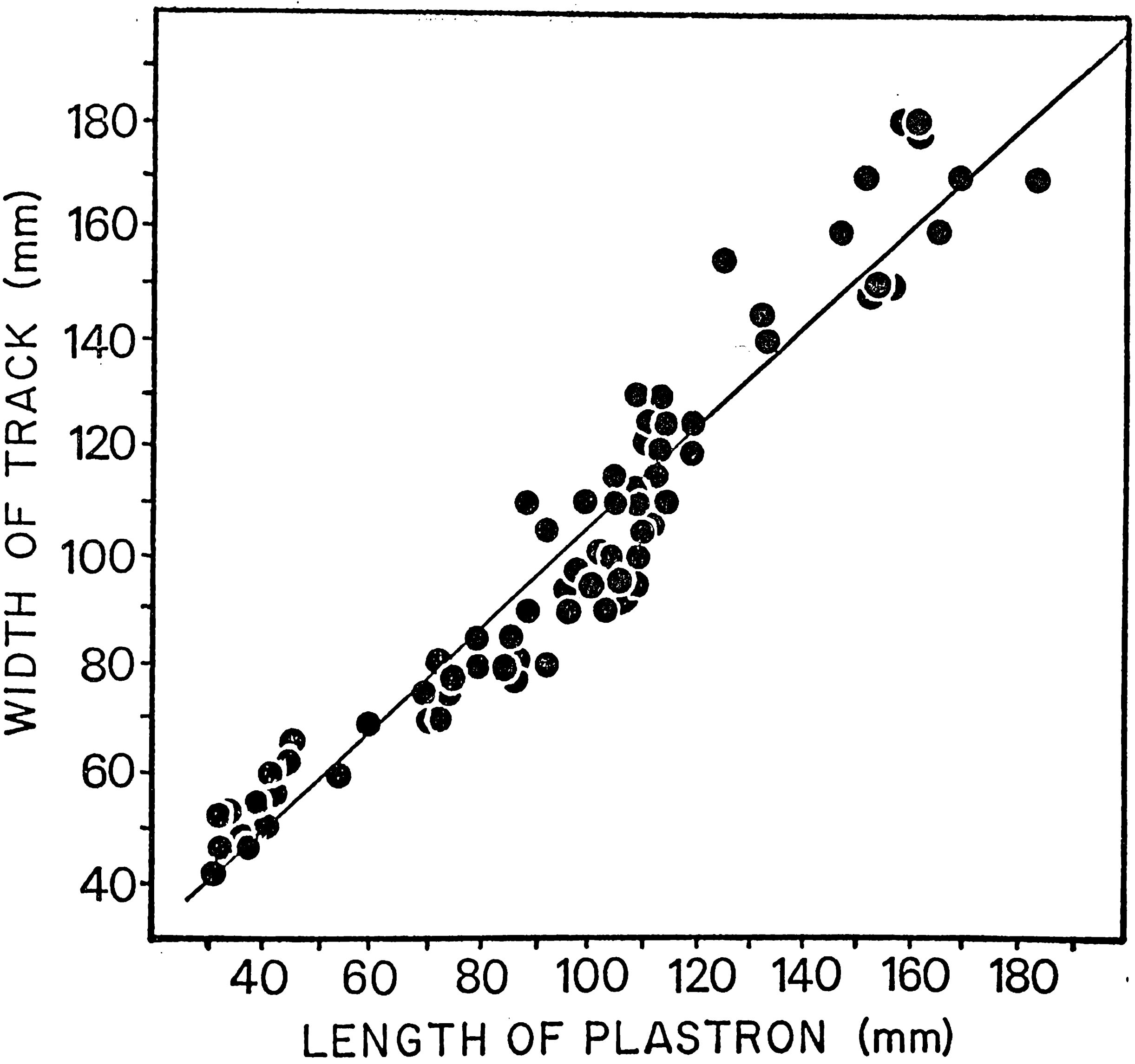
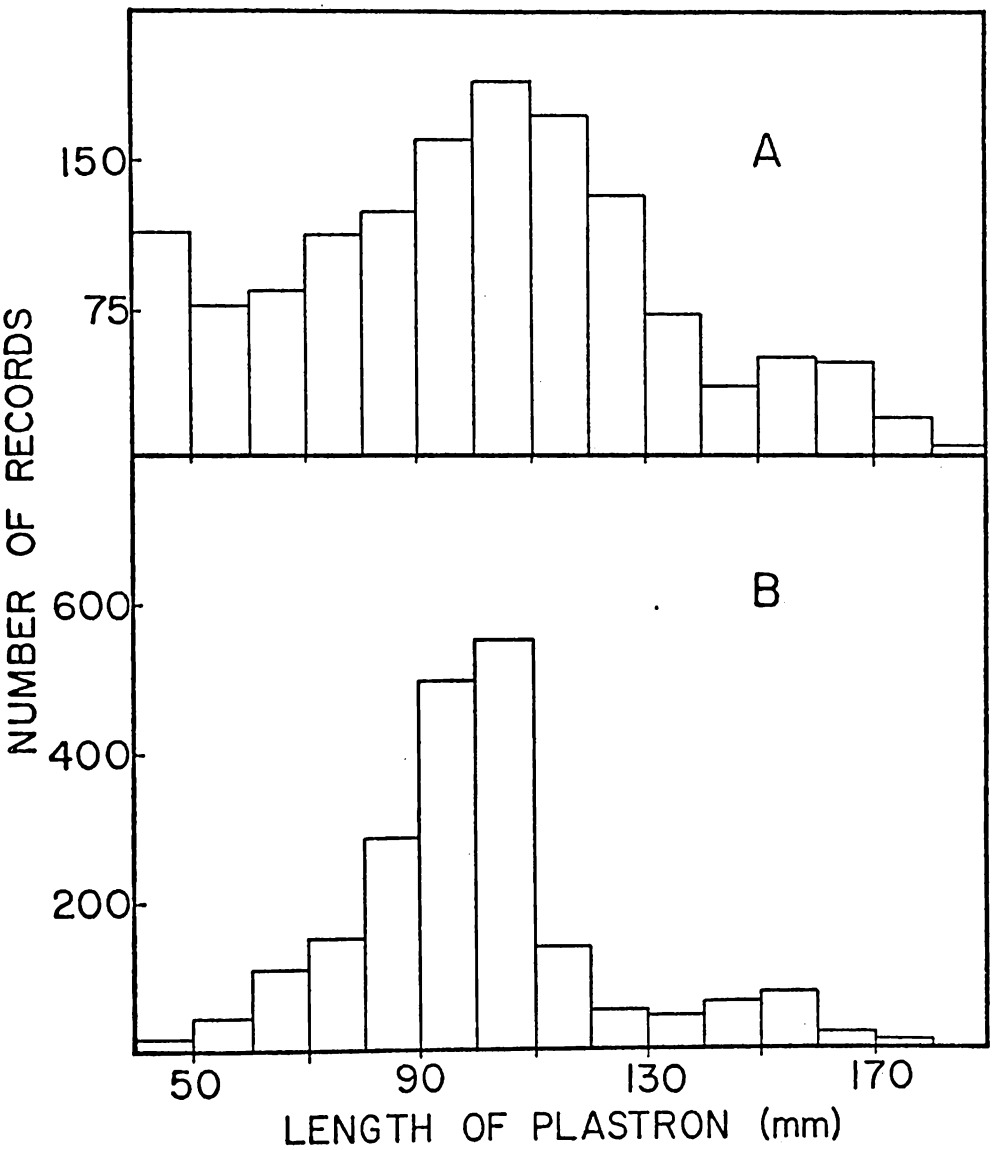

WIDTH OF TRACK (mm)
180
160
140
120
100
80
60
40
40
60
80
100
120
140
160
180
LENGTH OF PLASTRON (mm)

Fig. 6. Comparison of size distribution of captured turtles (B) to distribution predicted from tracks measured on the beach (A). A includes measurements taken throughout the season.


A
B
150
75
600
400
200
NUMBER OF RECORDS
50
90
130
170
LENGTH OF PLASTRON (mm)

In making counts I was always conservative to avoid duplications, and probably, I underestimated the numbers of individuals. Another reason B is more symmetrical is that track widths for individuals of a certain size are normally distributed resulting in normally distributed predictions of plastral lengths.

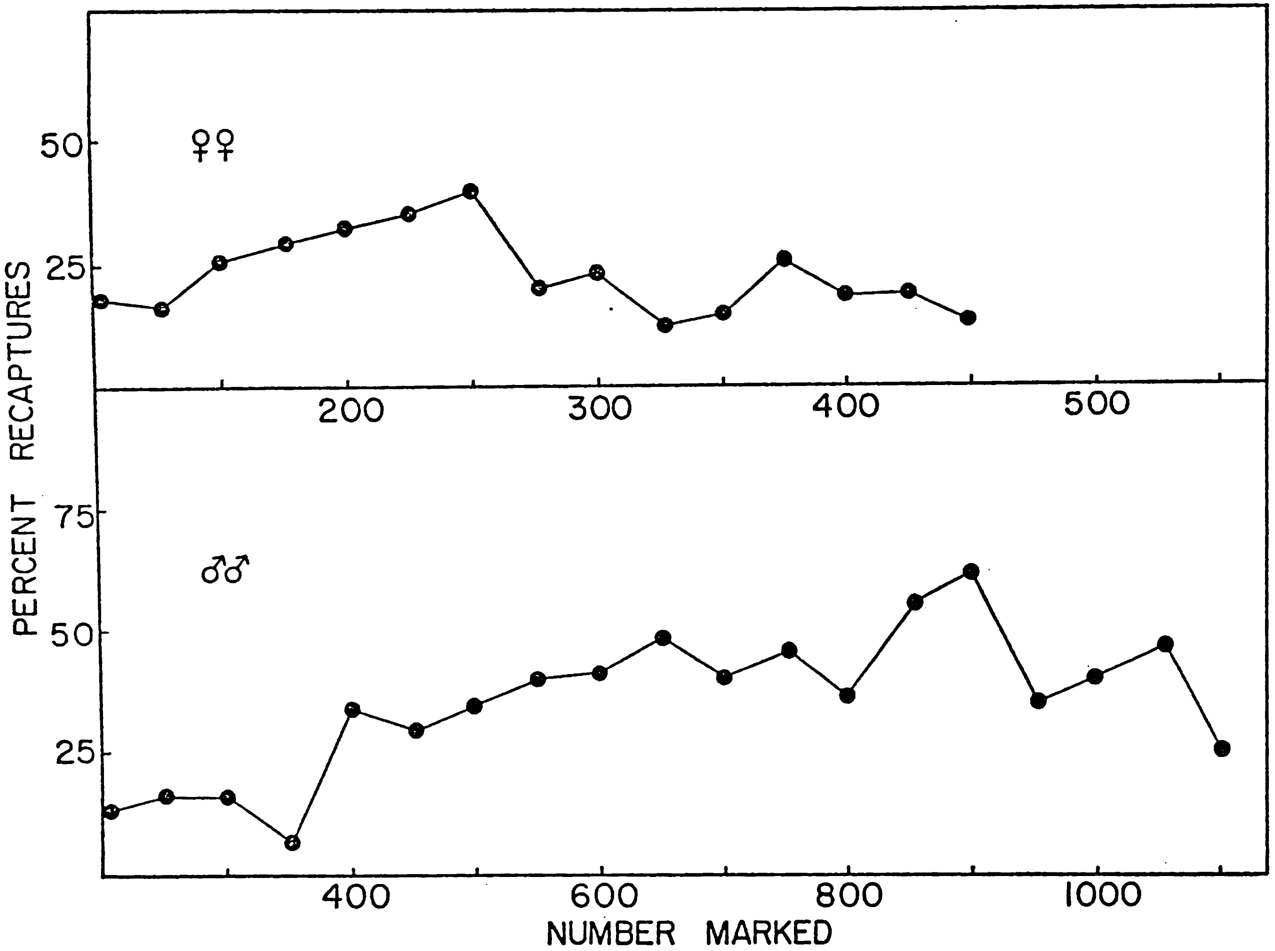
Size and spatial characteristics of the population. - Jolly's (1965) method was used to estimate the abundance of turtles on the main study area. Weekly estimates of proportion of recaptures (alpha), marked animals at large (M), and population size (N), were determined separately for males and females. All were characterized by a large amount of variability, especially the estimates of population size and the corresponding standard errors. In males (Table 3) changes as great as a ten-fold increase in population size were indicated during a single week, and even larger changes were indicated for females. Such large scale fluctuations could not be expected in such long-lived animals with slow population turnover. The fluctuations in census figures were especially puzzling since field observations indicated a more or less constant number of turtles. Numbers in 1974 appeared to be lower than in 1973, but this observation probably resulted from differences in activity levels and not from real changes in abundance.

Models for estimating size of populations based on capture-mark-recapture are most reliable if a high proportion of the animals are marked. Contrary to expectations, proportion of recaptures does not continue to increase as more turtles are marked (Fig. 7). Maximum ratios of recaptures to captures of unmarked individuals were reached fairly quickly and hovered just under 0.50 for males, and near 0.25 for females. The sampled population is continually

Table 3. Weekly population size estimates of males for the latter part of the 1973 field season.

Period	Alpha	M	Pop. size ± 2 S.E.
1	0.42	822	1943 ± 1797
2	0.29	332	1160 ± 959
3	0.56	281	506 ± 212
4	0.36	238	655 ± 413
5	0.30	476	1571 ± 803
6	0.35	441	1259 ± 746
7	0.47	486	1024 ± 421
8	0.50	441	882 ± 529
9	0.05	495	9405 ± 9397
10	0.45	1029	2287 ± 2671

Fig. 7. The relationship of percent of recaptures in samples to cumulative number of turtles marked.


♀♀
♂♂
50
25
75
50
25
200
300
400
500
400
600
800
1000
PERCENT RECAPTURES
NUMBER MARKED

being diluted with respect to marked individuals. Mortality among sub-adults and adults was believed to be low; five of 15 males found dead and one of six females found dead were marked. These proportions are slightly below proportions recaptured; therefore higher mortality on marked turtles should be ruled out as a cause of dilution. Recruitment by natality in this slow maturing, seasonally-breeding species could not possibly cause the continuous, high level dilution. Another possibility is that I only sampled a subset of a larger population. If individuals moved freely over a much larger area, then outward flow of marked turtles from the capture locations and influx of unmarked turtles could have caused continuous, high-level dilution. This situation would violate a basic premise of population size estimators using capture-mark-recapture -- that of equal probability of capture for all individuals. Table 4 shows the results of fitting the distribution of recaptures to a Poisson distribution with the null hypothesis of equal probability of capture once an animal is marked; the distribution is significantly different from expected. The larger than expected zero class probably represents transients or highly mobile individuals which have a low probability of recapture. Records with one or two recaptures probably are influenced by the same phenomenon, i.e., most turtles move freely over large areas yielding smaller than expected numbers of turtles which are recaptured one or two times. Classes with three or more recaptures have more individuals than expected; these primarily are males which are unusually sedentary. For example, two turtles were each recaptured nine times over periods of four and nine months, respectively. If distributions of recaptures of males, adult females, and subadult females are analyzed separately,

Table 4. Number of recaptures of all turtles fitted to a Poisson distribution. $\bar{Y} = 0.514$; $G = 229.77$ ($P < 0.001$).

Number of recaptures	Observed	Expected
0	1045	918
1	307	472
2	113	121
3	50	21
4	9	3
5	4	0
6	3	0
7	2	0
8	0	0
9	2	0

the results are similar in each case to the above, but means are lower in females than in males.

The Jolly method is refined to allow for movement into and out of the sampled area but requires that such movement be permanent. The method assumes three possibilities for an individual present at time $\underline{i}$ in the $\underline{i}$+1th sample: It may be recaptured; it may be still present but not captured; or it may not be captured because it has left the population permanently (Brussard and Ehrlich, 1970). These alternatives do not consider the possibility of temporary emigration. Table 5 demonstrates the correlation between elapsed time after marking and probability of recapture. This correlation suggests that turtles do return after leaving the area sampled, supporting the thesis that there is relatively free movement within a more extensive area. Plummer and Shirer (1975) monitored daily movement in this species, and found it to be extensive. Activities are centered in restricted home ranges, however, such ranges are shifted frequently and there appears to be no well-developed homing tendency. Home ranges are large, about 475 m in length for males and about 1225 m for females (almost the entire length of the main study area). One female moved almost 22 km in 20 days, passing through the main study area twice. Instances of turtles traveling beyond the limits of the main study area temporarily were noted, and movements of as much as 6 km up- and downstream from the main study area were recorded for adult females. Trapping records included those of many individuals that originally had been on the main study area, were recaptured several km distant, and were later recaptured again on the main study area.

Hence there is no doubt that individuals are capable of frequent and long movements. The Jolly estimates and recapture ratios shown in

Table 5. Proportion of turtles marked in various periods which were later recaptured. Period 1 = 1-31 May; 2 = 1 Jun. - 15 Jul.; 3 = 16 Jul. - 31 Aug.; 4 = 1-30 Sep. Males: $\tau = 0.91$ ($P<0.01$). Females: $\tau = 0.78$ ($P<0.01$). Numbers in parentheses are sample sizes.

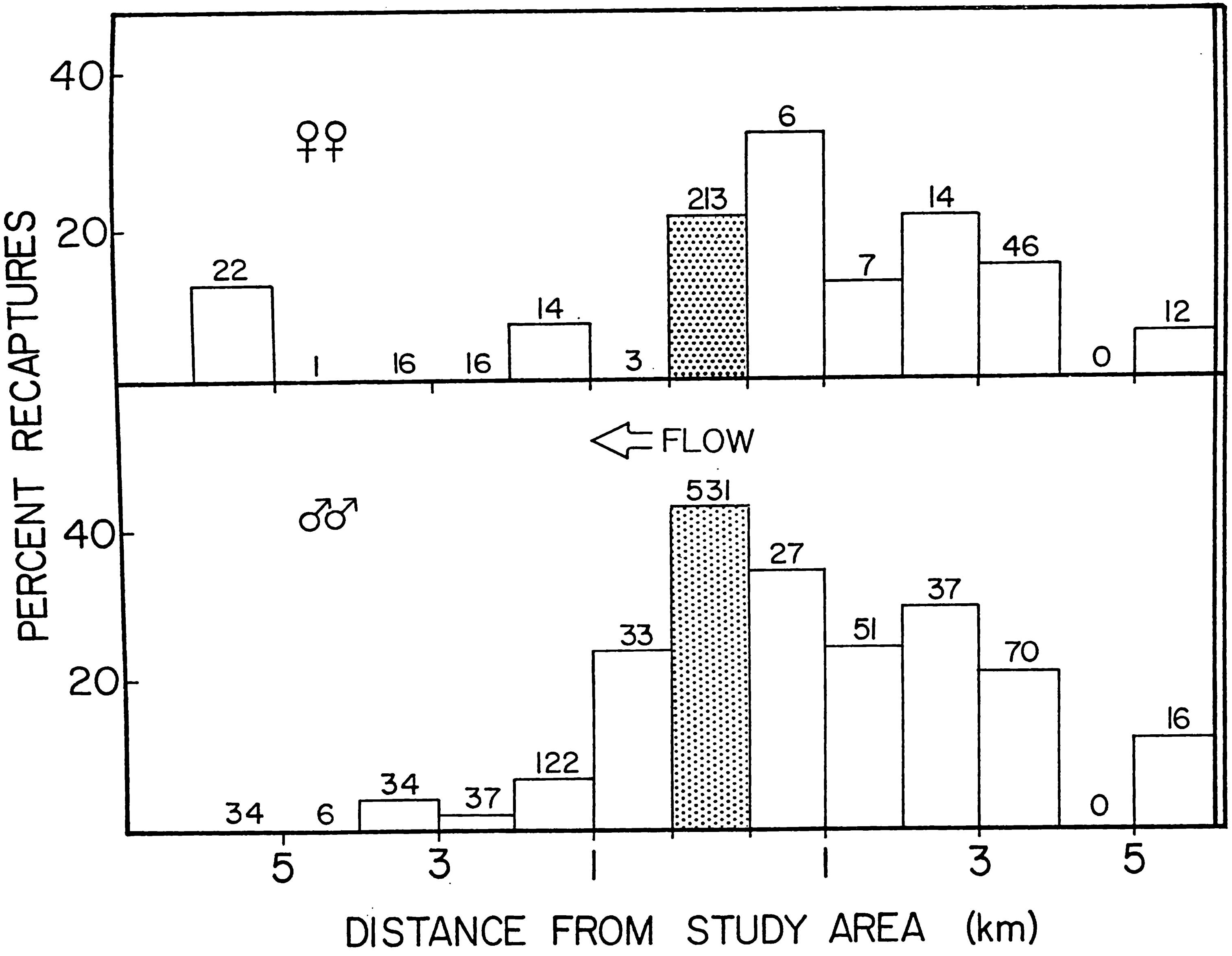
Period		Males	Females
1972	3	0.51 (209)	0.38 (90)
	4	0.64 (39)	0.37 (8)
1973	1	0.49 (228)	0.41 (17)
	2	0.42 (251)	0.30 (114)
	3	0.38 (169)	0.33 (52)
	4	0.24 (54)	0.13 (24)
1974	1	0.22 (53)	0 (23)
	2	0.21 (201)	0.08 (141)
	3	0.15 (72)	0.04 (25)
	4	0.16 (75)	0 (9)

Figure 7 suggest that a substantial proportion of the population engages in such movement. Figure 8 shows the proportions of recaptures of turtles marked on the main study area and later recaptured at locations up- and downstream from the main study area. Remarkably high proportions were found at distances up to 6 km from the main study area. Contingency table analysis indicates that virtually the entire 14 km length yielded proportions of females not significantly different from the main study area, but sample sizes were so small as to make interpretation difficult. Recapture proportions of males for distances extending from 1 km downstream from the main study area to 3 km upstream from it were not significantly different from the proportions on the area itself. The greater movement of females obviously influences these results so that for females there is greater variation in Jolly estimates, and lower recapture rate. The concentration of recapture records upstream from the study area evidently resulted from the presence of a dam preventing farther upstream travel whereas free movement downstream was possible.

More than 500 hatchlings were group-marked and released in the vicinity of the main study area, but only 3 of them were recaptured, and these were at a sandbar about 4 km downstream a few days after release. Passive dispersal must play an important role in their dynamics.

An accurate estimate of the number of turtles in this subpopulation is difficult to obtain. Direct counts even for small areas were unfeasible and indices based on capture-mark-recapture were biased because of the movement patterns. However, several different approaches yield figures of similar magnitude and serve to give a composite approximate estimate of the abundance of turtles greater than 60 mm in length.

Fig. 8. Percent of recaptures of turtles marked on the main study area during 1972-1973 which were recaptured during 1974-1975 at various distances from the main study area. Stippled bars represent main study area; numbers above each bar are sample sizes. Double line at right represents Bowersock Dam -- an absolute barrier to upstream movement.


♀♀
♂♂
PERCENT RECAPTURES
40
20
40
20
22
1
16
16
14
3
213
6
7
14
46
0
12
FLOW
34
6
34
37
122
33
531
27
51
37
70
0
16
5
3
1
1
3
5
DISTANCE FROM STUDY AREA (km)

In a similar situation with frequent movement from and into the area sampled, Brussard and Ehrlich (1970) estimated sizes of butterfly populations by averaging Jolly estimates over several sampling periods. They reasoned that the number of animals at large would fluctuate greatly over short time spans due to leakage; however, if M is averaged over longer periods, return of some marked animals that had left the sampling area would tend to compensate for leakage. Averages for the weekly estimates in Trionyx indicated a population with 1338 males and 463 females. The years 1972-1974 also were divided into 18 periods and 8 periods, respectively, for analysis by Jolly's method. This procedure should have the effect of damping the re-emigration phenomena; estimates generally were not as highly variable although standard errors remained high. If the estimates in these two analyses are averaged, the values are 1254 and 1279 for males and 566 and 946 for females, respectively.

Population size also was estimated by the Lincoln Index method with 1972-1973 as the precensus period and 1974-1975 as the census period. All of the data in each period were pooled so that there was one observation per turtle. Estimates were 2178 males and 1458 females. Because this method assumes a closed population, errors introduced by influx of new individuals and the leakage of marked individuals might be expected to result in census figures greatly inflated over the Jolly estimates. Hayne (1949) reasoned that the shorter the period between marking and re-sampling, the less would be the effect of movement into and out of the population. However, because short-term trapping periods are often highly variable in terms of proportions recaptured (true with Trionyx), Hayne proposed a method of averaging short-term estimates which should give more realistic estimates of population size. His method is based upon computing the reciprocal of the slope of the regression line describing the relationship between proportion of recaptures to the number of marked animals in the population (Fig. 7). Because rate of dilution exceeded marking rate in 1974-1975 (after about 850 males and 250 females were marked), a negative slope is produced which greatly overestimates population size if the entire period of study is used in the calculations. However, in 1973, slopes gradually increase in both sexes, yielding estimates of population size of 1610 males and 641 females for the entire season and 1180 males and 582 females for the period 1 May - 15 July. Estimates fluctuate greatly if calculated for shorter periods but are dampened at periods of 2.5 months or greater. Because dilution of marked proportions occurs constantly, and not just between seasons, these estimates may still be inflated. These estimates plus the similarity of the three Jolly estimates for males inspires some confidence in the probability that there are about 1300 on the study area. The number of females is more difficult to judge due to inadequacy of the samples but probably there are about 500 present. Two of three Jolly estimates suggest this as do the Hayne estimates. If these estimates of male and female numbers are accepted a sex ratio of 2.6♂♂:1♀ is obtained approaching the 1.98:1 ratio derived from capture data.

These estimates agree with field observations. Eighty-eight turtles once were counted basking within a 100 m length of sandbar; at the same time, a large, but undetermined number of heads were visible in the adjacent waters. In early season, small sandbars appear to be literally covered with basking turtles. These observations and the large numbers of turtles caught in one trap or hand collected in small areas mentioned previously demonstrate high population densities.

DISCUSSION AND CONCLUSIONS

Most field studies of population ecology of small vertebrates assume that emigration and immigration play minor roles in the dynamics of the population and therefore usually are ignored. Investigators studying fresh water turtles have commented on the turtles' sedentary nature, well-defined local populations, fidelity to home pond, or some similar description. For example, Gibbons (1968) found that Chrysemys picta occurred in discrete local populations with minimal movement into and out of the population consequently, having little effect on estimation of population size. Indeed, except for periods of environmental stress forcing them to seek more favorable conditions (Cagle, 1944) freshwater turtles have been thought to confine their activities to fairly small areas.

That populations may respond differently to different environments is becoming well established. Tilley (1974) demonstrated that populations of the salamander, Desmognathus ochrophaeus separated by only 145 m responded demographically to different environments. Differences in diet between pond and river populations of Pseudemys scripta caused differences in age and size at maturity (Gibbons and Tinkle, 1969). Brussard and Ehrlich (1970) have shown that closely related species of butterflies may occur either in discrete local populations with little interpopulational movement or in vast, effectively panmictic populations covering hundreds of square kilometers with free movement within.

Basic differences between pond and stream environments might be reflected in structure of their turtle populations. In streams lack of physical barriers and the potentiality for passive dispersal by currents could result in large exchanges between local populations. Alternatively, any "population" of a manageable size for an ecological study may be only a subset of a much larger, ill-defined population in which individuals move freely. This appears to be the situation in riverine populations of T. muticus. I undertook the present study with the intention of making a detailed analysis of a "population" definable as the aggregate of turtles in preferred habitat of a 1.5 km section of river. This area presumably defined a natural population and the concept was consistent with descriptions of turtle populations in the literature. It now is clear that my "population" was not a natural unit; the true population extends over several km and apparently is not subdivided. Over 200 turtles were collected, primarily at a sandbar 6 km downstream from the main study area, and dissected for investigations of size at maturity and reproduction (Plummer, 1975a). Some of these turtles, particularly adult females, probably were integral members of the population sampled at the main study area. These individuals were included in size structure analyses (Figs. 4 and 6). It would require massive team efforts to adequately study dynamics of such populations by conventional capture-mark-recapture techniques.

Such conclusions may have broad implications. One of the initial objectives of any field study in population ecology should be to delimit those aggregates of individuals which function as genetic and dynamic units (Brussard and Ehrlich, 1970). If this is not done, then conclusions concerning population phenomena (e.g., factors involved in regulation of numbers, electrophoretic patterns) may be subject to question. These and other implications are discussed by Ehrlich, et al. (1975).

Little is known concerning the ecology of turtles in lotic environments. Recently, Hynes (1972) emphasized that, in general, much less ecological research has been done in rivers and streams than in lakes and ponds. Hynes states of the non-piscine vertebrates: "...we know very little about their place in the running water community and much of our knowledge remains in the natural-history stage of development." Freshwater turtles often attain high population densities as shown by the present study and by Cagle (1950), Sexton (1959), and Gibbons (1968). Even the aquatic Terrapene coahuila attains much higher population densities than its terrestrial congeners (Brown, 1974). By the criteria of biomass, turtles certainly ought to be considered important members of aquatic communities, and work is needed in order to determine their role. Particularly, investigations should be made of populations and communities in lotic environments.

SUMMARY

A riverine population of Trionyx muticus was studied for three years by capture-mark-recapture; about 3700 captures were made on 2700 individuals. These turtles are most active from May through September. Trapping success is affected by changes in water level, and a midsummer period of inactivity is associated with low, stable water levels and high water temperatures. Males prefer areas associated with emergent sandbars but females prefer deeper, more open

water except during the nesting season when they move into the shallow water adjacent to sandbars. Several types of activity are concentrated in specific microhabitats on sandbars. Deviations from parity in sex ratios were attributed to biases in sampling. About 82% of the male population and 25% of the female population was mature. Sizes of tracks on the beach may serve as a basis for estimating size structure of the population. There was a high degree of mobility within and between local subsets of the population; discrete populational boundaries were not observed. Approximately 1800 turtles were estimated to be within a 1.5 km section of river. However, direct counts of all individuals present were not feasible even for small areas, and indices based on capture-mark-recapture were biased by emigration and immigration. Such populational attributes cause difficulties in study by traditional methods.

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III. REPRODUCTION AND GROWTH

INTRODUCTION

Biology of trionychid turtles has not been studied in depth. Webb (1962) summarized the biology of the North American species, mainly from short reports. Trionyx muticus is one of the least known North American species; aspects of its reproduction and growth have been reported by Muller (1921), Cahn (1937), Goldsmith (1944), Anderson (1958), Webb (1962), Fitch and Plummer (1975), and Plummer (1976). I studied reproduction and growth in a population of T. muticus from July 1972 to May 1975. This report expands a preliminary report on the same population by Fitch and Plummer (1975).

METHODS AND MATERIALS

Turtles were collected from a 14 km section of the Kansas River near Lawrence, Douglas County, Kansas, approximately 39° N. Further description of the area and habitat have been recorded in other reports (Fitch and Plummer, 1975; Plummer and Shirer, 1975; and Plummer, 1975a; 1975b). Turtles were captured by hand or in wire mesh funnel traps, marked and released. Some were preserved for dissection. Approximately 3700 captures were made on 2700 turtles; 104 males and 102 females were dissected. Turtles were measured with a plastic ruler to the nearest 0.5 mm and weighed on spring scales to the nearest 5 gm in the field. In dissected females number and size of ovarian follicles, number of shelled oviducal eggs and corpora lutea, and widths of oviducts were noted; in males, size and condition of testes, and appearance of vasa deferentia were determined. Volume of testes was computed from the formula for an ellipsoid. All measurements in the laboratory were made with dial calipers. Water temperatures were read from a Taylor maximum-minimum thermometer.

Body size is expressed as length of plastron (PL). The posterior edge of the carapace is subjected to mutilation and its flexible nature and curvature render it less suitable for precise measurement than the plastron. Mean carapace length/plastron length (CL/PL) remains relatively constant (1.34-1.40) throughout ontogeny (Fitch and Plummer, 1975), so that either length of carapace or length of plastron is an accurate indicator of body size. Length of plastron is measured midventrally from the posterior edge to the anterior edge, including the marginal cartilaginous portion.

RESULTS AND DISCUSSION

Size at sexual maturity. - Criteria used for determining sexual maturity in males were: coiling of vasa deferentia, extension of cloaca beyond the posterior edge of the carapace, or testes volumes greater than 100 mm^3; criteria for females were: presence of oviducal eggs, corpora lutea, or follicles with diameters greater than 15 mm. Mature females have fleshly, convoluted oviducts generally 12-15 mm wide; two subadults approaching maturity (148, 151 mm) had straighter, membranous oviducts 7-8 mm wide.

All males greater than 90 mm (n = 70) met all three criteria for sexual maturity except for one of 91 mm which had enlarged testes and convoluted vasa deferentia, but the cloaca was short of the posterior edge of the carapace by 4 mm. This turtle had a CL/PL value of 1.43

as compared to the average 1.38 for *T. muticus* (Fitch and Plummer, 1975). Thus, some young adults with high CL/PL ratios would not have cloacas extending beyond the edge. Seven of 8 males of 86-90 mm met all three criteria. The largest immature male (90 mm) had testes measuring 2.0 x 10.5 mm (vol. = 22.0 mm^3), and extremely small, straight vasa deferentia, and the cloaca was 11.0 mm anterior to the edge of the carapace. Eight of 11 males of 81-85 mm met all three criteria; another of 82 mm was clearly immature and two (81 and 84 mm) appeared to be approaching maturity with testes volumes of 80.2 and 89.8 mm^3, respectively, but they still had straight or only slightly convoluted vasa deferentia and had cloacas that failed by 4 and 8 mm to reach the carapacial edge. Of four males in the 76-80 mm class, two (79, 80 mm) were clearly mature whereas two (77, 80 mm) were clearly immature. All males less than 76 mm were immature. Most males appear to mature at plastral lengths of about 80-85 mm. Webb (1962) indicated a range of 82-92 mm for maturing males.

The smallest mature female (131 mm) contained three shelled eggs but no ova in the 6-20 mm categories on 30 June. Five females of 134-138 mm were clearly immature, containing ova in the 1-5 mm class only. One female of 135 mm had 15 ova of about 13 mm in May. Two of four females of 143-145 mm in May-June contained enlarged, preovulatory follicles (16-20 mm). Four of five females of 140-145 mm obtained August-September contained follicles in the 11-15 mm class and apparently were nearing maturity, or were mature, having ovulated all follicles in the 16-20 mm class. Three of six females of 146-150 mm were mature. One female of 151 mm was immature, but all turtles larger than 151 mm were mature. Thus, it seems that most females mature at plastral lengths between 140 and 150 mm, slightly smaller than indicated by Webb (1962).

Secondary sex characteristics. - Mean plastral length of mature males was 98.2 ± 0.24 mm (n = 1162); that of mature females was 154.2 ± 0.66 mm (n = 173). In most mature females a blotched or mottled carapacial pattern has replaced the juvenile pattern of small, ill-defined dots and short streaks. Some individuals retain this juvenile pattern after they have matured. One had retained it at a length of 155 mm, and retention in smaller adult females is not uncommon. Development of blotched patterns is not usually synchronized with attainment of sexual maturity; the majority of females of 90-100 mm had blotched patterns as well as did one of only 59 mm. Webb (1956) demonstrated that juvenile T. spiniferus emoryi also develop blotched patterns. All male T. muticus captured retained the juvenile pattern.

The length of the preanal region of the tail increases gradually with body size in females (Fig. 1). In most mature females the cloaca does not approach the posterior edge of the carapace, but in some it is even with the edge because of an unusually long preanal region or an unusually short carapacial edge. Webb (1962) stated that in some large females of T. muticus the cloaca extends a short distance beyond the posterior edge of the carapace. Preanal length in males increases gradually in early development and then abruptly elongates as maturity is reached (Fig. 2), so that usually the cloaca extends beyond the posterior edge of the carapace 1-17 mm. Webb (1956) demonstrated these same relationships between preanal length and plastral length in males and females of T. s. emoryi.

In juveniles 60 mm or larger the tails of males often are slimmer than those of females, which have a more pyramidal shape. This

Fig. 1. The relationship of pre-anal length and body size in female _T. muticus_. Closed circles are immature females; open circles are mature females.

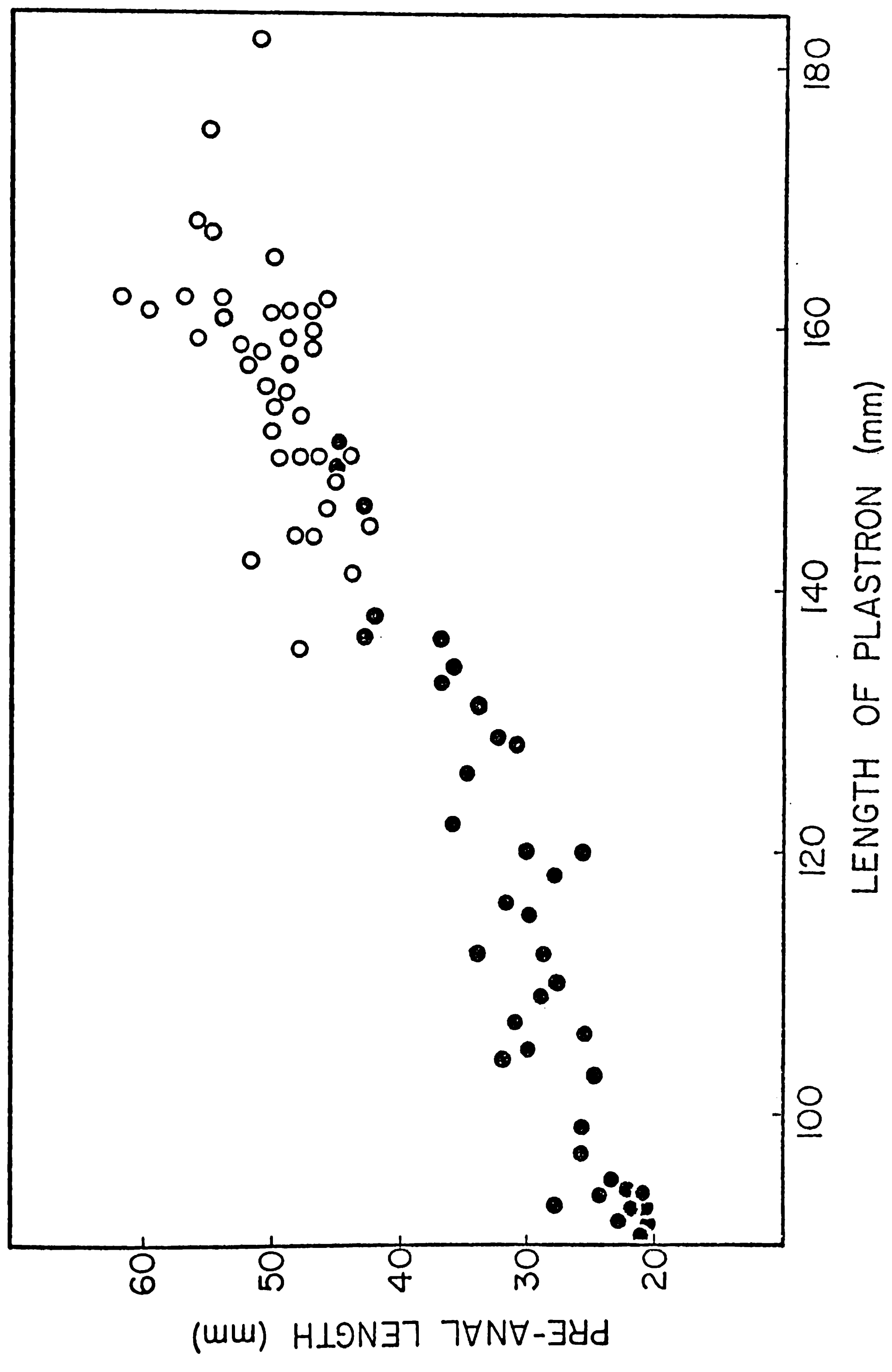
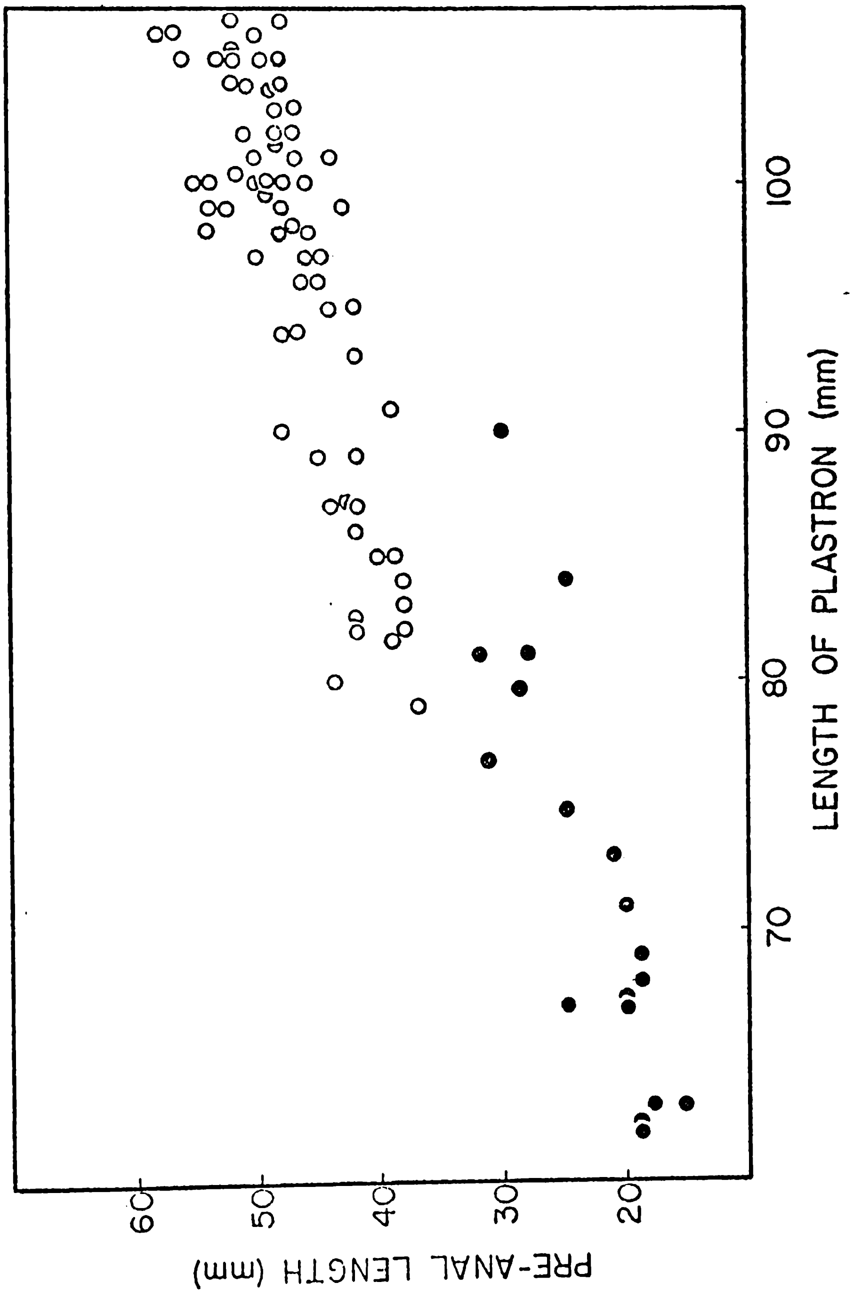

PRE-ANAL LENGTH (mm)
60
50
40
30
20
LENGTH OF PLASTRON (mm)
100
120
140
160
180

Fig. 2. The relationship of pre-anal length and body size in male _T. muticus_. Closed circles are immature males; open circles are mature males.

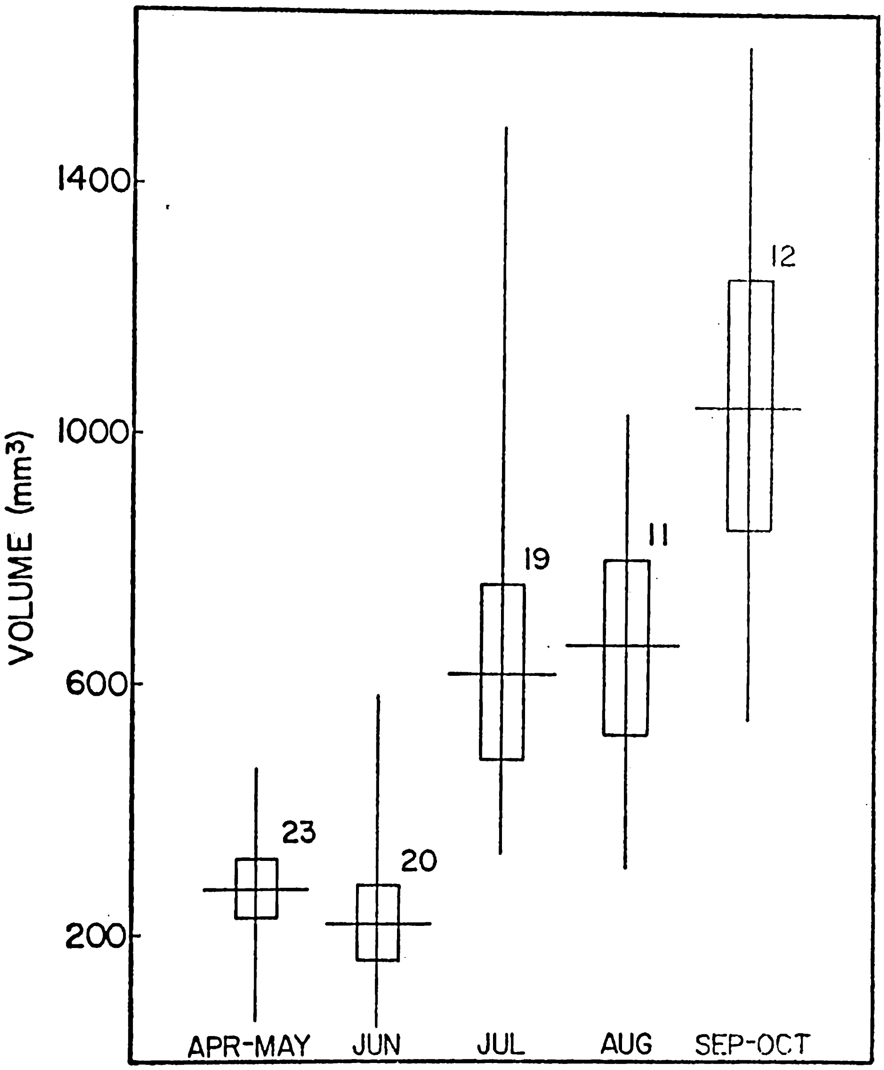

PRE-ANAL LENGTH (mm)
60
50
40
30
20
LENGTH OF PLASTRON (mm)
70
80
90
100

difference permits fairly accurate sexing of juveniles between 60-65 mm; seven of eight dissected had been correctly sexed. Sexual dimorphism in tail shape usually is obvious above 65 mm.

Reproductive cycle of males. - Mature testes are whitish, elongate ellipsoidal organs with maximum diameters 3-10 mm, lengths 12-31 mm, and volumes 100-1600 mm^3, depending upon time of season and size of turtle. In immature turtles testes vary with size of turtle but generally are less than 2 mm in diameter and 10 mm in length, and are flatter, more ribbon-like, and more translucent than mature testes.

The volume of mature testes varies seasonally (Fig. 3); they are at maximum size before hibernation, decrease in size in spring and then abruptly increase in size in mid-summer. In April-May all of 23 turtles had vasa deferentia about 2 mm in diameter, highly convoluted and filled to turgidity with a milky white fluid. In June vasa deferentia began to appear less engorged, flacid, and translucent. Several appeared completely empty. Six of 20 had this flacid appearance in June, as did 14 of 19 in July, and 10 of 11 in August, but only 4 of 12 in September-October. Apparently these changes in appearance correspond to different stages of the spermatogenic cycle. Spermatogenesis probably begins in summer with the testes progressively enlarging to reach maximum size just before hibernation. Sperm are released into accessory organs in fall and probably are retained in them until mating the following spring. During spring testis size is decreased by movement of sperm into accessary organs as the vasa deferentia are emptied in the mating process. T. muticus has a spermatogenic cycle similar to those described for other North American turtles including Sternotherus (Risley, 1938), Terrapene (Atland, 1951), Chrysemys (Gibbons, 1968), and Chelydra (White and Murphy, 1973).

Fig. 3. Volumetric changes in mature testes of *T. muticus* throughout the season. Horizontal lines are means; vertical lines are ranges; rectangles delimit 95% confidence limits; numbers are sample sizes.


VOLUME (mm³)
1400
1000
600
200
12
11
19
23
20
APR-MAY
JUN
JUL
AUG
SEP-OCT

Reproductive cycle of females. - In 27 shelled oviducal eggs from five females, yolks averaged 17.3 ± 0.18 mm (range 16.0-19.0) in diameter. Enlarged ova (16-20 mm) occurred in distinct sets in each adult collected from May-June (n = 34). Three females collected 10 May contained only enlarged ova, but one collected on 22 May and all those collected in early June contained both enlarged ova and corpora lutea indicating that ovulation probably occurred in mid-May. Enlarged ova were conspicuously absent from adults collected from late July to early September (n = 10), but were present in three of four collected in late September.

Numbers of ova in different ovarian size classes varies seasonally (Table 1). Number of enlarged ova is largest in May and is reduced by ovulation in June; by July all viable enlarged ova have been ovulated. Enlarged ova appear again in September. Both the 6-10 mm and the 11-15 mm classes increase in numbers from May-June to July-September as ovarian enlargement progresses in preparation for egg production in the following year. Follicles in the 1-5 mm class generally were numerous throughout the season. Occasional atretic follicles, dark orangish-brown and hard to the touch, were found in all follicular size classes throughout the season.

In a female collected 22 May ovulation apparently had recently occurred; the reddish-brown corpora lutea were 9-10 mm in diameter. Corpora lutea were whitish and 6-8 mm in diameter in females collected immediately after oviposition and in those that had shelled oviducal eggs. In 5 females collected 27-28 June, there were two sets of corpora lutea; those of the larger set apparently corresponded with recently ovulated ova (in 3) or in recently oviposited eggs (in 2). Those of the smaller set, translucent and 3-5 mm in diameter, apparently corresponded to previous clutches. One female, collected

Table 1. Number of ovarian follicles in females dissected throughout the season.

Dates	Diameter of ova (mm)		
	6 - 10	11 - 15	16 - 20
May (n=5)	2.0 ± 2.0	4.8 ± 2.21	18.0 ± 2.44
Jun. (n=29)	3.3 ± 0.76	1.3 ± 0.29	10.9 ± 1.39
Late Jul. - Aug. (n=7)	9.4 ± 1.61	8.1 ± 3.43	1*
Sep. (n=5)	8.4 ± 1.50	9.8 ± 2.59	9.8 ± 4.07

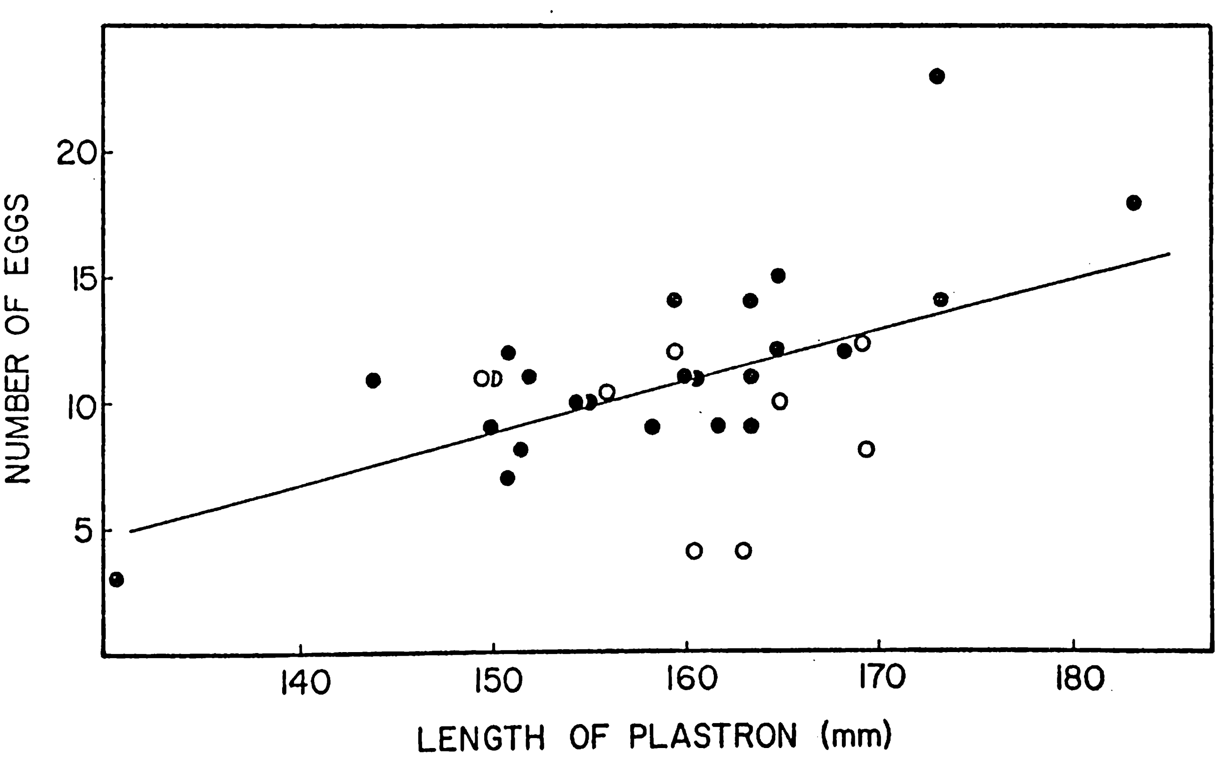
*Atretic

26 July, had colorless corpora lutea about 4-5 mm in diameter. Females collected in August and September did not have corpora lutea discernable by gross inspection.

Migration of ova to the contralateral oviduct was indicated in 10 of 15 turtles by non-correspondence between number of corpora lutea and number of oviducal eggs on their respective sides. Dobie (1971) found similar non-correspondence in Macroclemys. Moll and Legler (1971) summarized the literature pertaining to extra-uterine migration in turtles.

Clutch size. - From 199 nests examined in the field, Fitch and Plummer (1975) determined clutch size to be 12.6 ± 0.30 (range 1-29). By the same criteria I determined clutch size to be 10.4 ± 0.31 (range 3-26) in 102 nests. This difference is significant ($P<0.001$), and is at present inexplicable, except as a result of fluctuating environmental conditions from year to year. The shelled oviducal eggs present at one time presumably represent a clutch. The oviducal complement in 22 females dissected was 11.8 ± 0.76 (range 3-23). To account for the unusually small number of eggs occasionally found in nests, Fitch and Plummer (1975) suggested that possibly T. muticus distributes a clutch in more than one nest. I found one female (163 mm) still near her recently completed nest which contained four eggs, but dissection revealed 12 corpora lutea of approximately the same size, and 13 ova in the 16-20 mm class. One female (131 mm) had only three shelled oviducal eggs and three corpora lutea. Because clutch size is positively correlated with body size (Fig. 4), unusually small numbers of eggs in nests may also represent females in their first nesting season. Muller (1921) and Cahn (1937) both stated that clutch size is related to body size in T. muticus, but neither presented supporting data.

Fig. 4. The relationship of clutch size to body size in _T_. _muticus_. The regression equation is $\bar{Y} = -21.5 + 0.20X$ ($P<0.001$). Closed circles are data determined by dissection; open circles are data gained through examining natural nests.


NUMBER OF EGGS
20
15
10
5
OD
140
150
160
170
180
LENGTH OF PLASTRON (mm)

Clutch size in natural nests in June was 11.1 ± 0.48 (n = 53), whereas in July it was 9.3 ± 0.65 (n = 24). The difference is significant ($P < 0.05$). Unfortunately, females collected in July for dissection did not contain shelled oviducal eggs or corpora lutea of sufficient size to determine the ovarian complement, but mean oviducal complement from dissected turtles in June (11.8) was similar to the estimate of June clutch size in natural nests (11.1). Fitch and Plummer (1975) reported significantly larger clutch sizes in June than in July. For a given female, the first clutch probably is larger than succeeding clutches.

Reproductive potential. - Reproductive potential is the number of eggs a female is capable of producing in one year (Gibbons, 1968). Ova of 16-20 mm, plus the eggs actually laid, and the shelled oviducal eggs (or the corpora lutea representing the last two categories) may provide a total count of eggs produced. This procedure assumes that few enlarged ova become atretic, which seems to be true in T. muticus. Reproductive potential in 32 turtles averaged 25.7 ± 2.01 (range 10-62), or the equivalent of a little over two clutches. Reproductive potential is positively correlated with body size (Fig. 5); probably small adults produce one clutch per year whereas larger adults produce more than one (Table 2).

In 1974 ovulation probably began in mid-May and oviposition began on 27 May, suggesting retention of eggs for about two weeks. Similar retention intervals have been reported in Terrapene (Legler, 1960) and Chrysemys (Gibbons, 1968). The length of the nesting season of T. muticus is at least 40-45 days (Plummer, 1975b), long enough for two or more clutches to be laid by the same individual. Each mature female dissected during the nesting season contained eggs and/or corpora lutea.

Fig. 5. The relationship of reproductive potential to body size in *T. muticus*. The regression equation is $\bar{Y} = -81.1 + 0.67X$ ($P<0.001$).

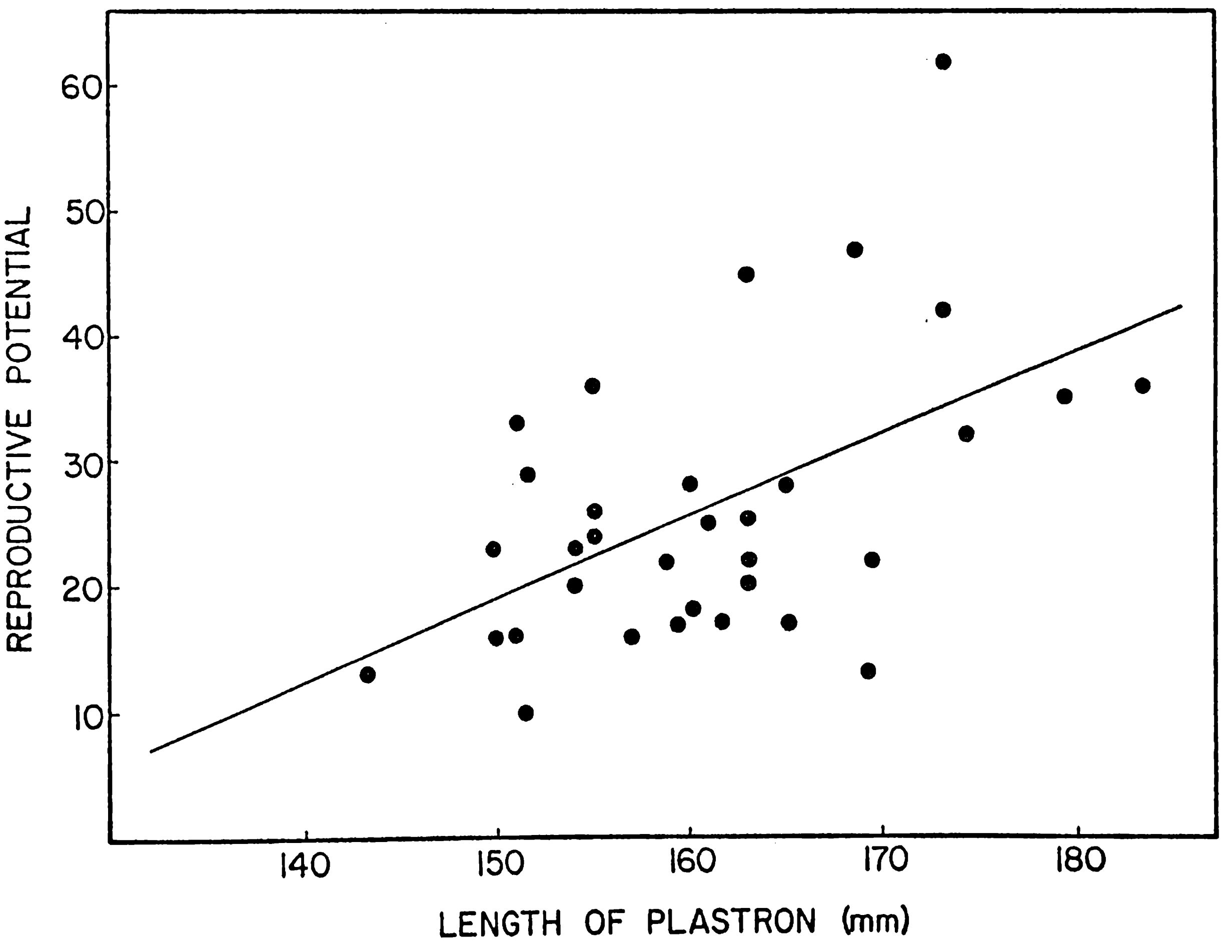

60
50
40
30
20
10
REPRODUCTIVE POTENTIAL
140
150
160
170
180
LENGTH OF PLASTRON (mm)

Table 2. Selected examples of females which potentially would have produced more than one clutch in a season.

Date	PL (mm)	oviducal eggs	corpora lutea	enlarged ova	eggs laid
22 May	165	15	15	14	- - -
5 Jun.	179	14	14	21	- - -
15 Jun.	168	0	12	35	12
20 Jun.	155	10	10	26	- - -
27 Jun.	163	0	12	13	4

Thus, each mature female in the population probably breeds annually, with a reproductive potential of about 20-25 eggs.

Muller (1921) reported an average clutch of 22 from natural nests of T. muticus in Iowa. Cahn (1937) reported clutches of T. muticus from Illinois usually ranging from 18-22, with a maximum of 31. Goldsmith (1945) reported average clutch sizes of about 18.6 from natural nests of T. muticus in Iowa. Anderson (1965) reported clutches numbering approximately 20 for T. muticus in Missouri. Webb (1962) dissected six T. muticus from more southern latitudes (below 36.5°) and found only 3-9 oviducal eggs but a larger number of enlarged follicles. He also found that numbers of eggs in nine nests ranged from 5-15 (mean 7.7). Webb suggested a latitudinal gradient in clutch size and number of clutches similar to that found in other turtles (e.g., Sternotherus; Tinkle, 1961), but he perceptively cautioned that there may not be great differences in reproductive potential between northern and southern populations because of variation within a given area. In my study clutch size was notably smaller than those previously reported for the same general geographic area. Inasmuch as both clutch size and reproductive potential is correlated with body size and apparently maximum female body size is potentially much larger than in my study (see growth section), perhaps clutch size is smaller because the population is young. If the largest female grew at an average rate, she would be only 16 years old. No indications of senility was found in any turtle dissected.

Growth. - Growth was studied by examining size classes in hatchlings and yearlings and by direct measurement of growth in individually marked turtles. Generally, a minimum interval of two months between captures was required for sufficient growth to occur to overcome the small random errors in measurement. About 365 recaptures on 348 males and 83 recaptures on 75 females were useful in growth analyses. If a turtle was recaptured more than once, with each interval between captures extending over several months, the growth rates for each period were considered individually. However, such instances were rare, so that usually an individual yielded only one record of growth rate. Turtles were grouped into 10 mm size classes (or 5 mm classes for adult males in which sample sizes were large). If an individual growth record involved progression from one size class to another, the record was used only for the class of the original capture. Growth rates tend to decrease with size of turtle, therefore this procedure would tend to slightly decrease the mean growth rate recorded for the original class. However, records of this nature were relatively few. Most activity is concentrated from May through September (Plummer, 1975a), and this coincides with the period of growth observed in individuals.

Growth of juveniles. - Length of plastron in 142 hatchlings averaged 24.5 ± 0.17 mm (range 19.5-28.8). The length of the nesting period extends from late May to mid-July and the subsequent emergence of hatchlings extends from early August to late September (Plummer, 1975b). Turtles hatching early in the season would grow almost two months before hibernation whereas turtles hatching in late September would make little or no growth before entering into hibernation. The range in hatchling size and the time of hatching therefore are important parameters in determining the size at which a turtle enters into its first full season of growth in May.

Several hundred hatchlings were marked during the course of the study, but none was ever recaptured after periods long enough to reveal growth. Samples of small turtles which seemed to be yearlings were grouped at different times of the season in order to show the increasing size of cohorts (Table 3). Average size increased as the season progressed, but range of sizes was great in all groups, and young as small as 26 mm could be found as late as mid-June. Young averaged 35.1 mm by mid-June having increased by 43% over the size of the average hatchling. Fitch and Plummer (1975) calculated an increase of approximately 36% (CL) during this same period of months in other years. By mid-September yearling cohorts average 47.1 mm. There probably is little growth during late September; size of yearlings at the end of the first full season of growth probably is about 48 mm. Turtles have approximately doubled their size at an age of one year. If an average growth period of one month is allowed for hatchlings, one-year-olds have grown for about six months at an average monthly growth rate of about 3.8 mm. One individual of 43.5 mm captured on 10 August 1973 was recaptured on 26 September 1974 at a length of 73.5 mm. Growth was 30 mm in 6.5 growth months or 4.6 mm per month. If a period of 1.5 growth months is allowed for this turtle after its capture in 1973, then it would have grown to 50.4 mm before hibernation. Its growth rate slightly exceeded the average.

Fourteen juveniles in the 48-60 mm class were recaptured and their mean monthly growth rate was 2.9 ± 0.32 (range 1.0-5.38). At a length of 60 mm or more turtles may be sexed; separate analyses reveal different growth patterns for the two sexes.

Growth of males. - Growth in male turtles (Table 4) is slower than in hatchlings or juveniles, with monthly increments of approximately 2 mm until maturity is reached at about 80 mm. Growth abruptly decreases after maturity is reached and apparently becomes asymtotic in old

Table 3. Size of yearling cohorts at various times of the season.

Date	Mean PL (mm)	N
Late May	30.1 ± 0.50	24
Mid-Jun.	35.1 ± 0.58	54
Mid-Jul.	38.5 ± 3.00	2
Early Aug.	44.6 ± 1.01	9
Late Aug.	45.4 ± 0.64	18
Mid-Sep.	47.1 ± 1.32	5

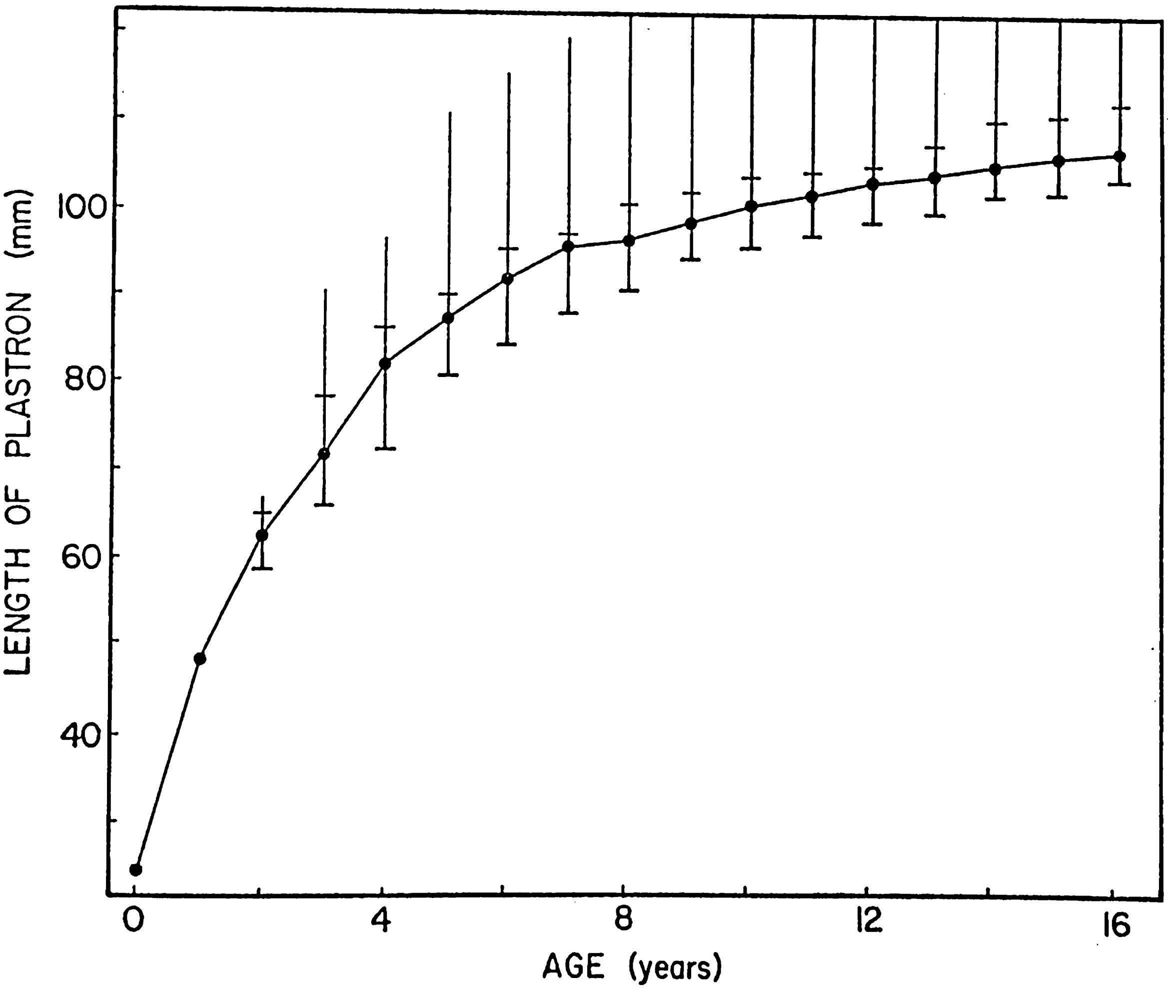
Table 4. Growth rate in male *T. muticus*.

PL	N	$\bar{Y}$	$\bar{Y} \pm 2$ S.E.	Range
61 - 65	10	1.95	1.15 - 2.75	0.67 - 2.33
66 - 70	16	2.17	1.27 - 3.07	0 - 6.67
71 - 75	20	2.48	1.94 - 3.02	0.50 - 5.71
76 - 80	20	1.92	1.36 - 2.48	0.29 - 4.52
81 - 85	35	1.03	0.77 - 1.29	0.09 - 3.08
86 - 90	41	1.18	0.78 - 1.58	0 - 6.67
91 - 95	46	0.73	0.55 - 0.91	0 - 3.00
96 - 100	56	0.37	0.27 - 0.47	0 - 1.67
101 - 105	65	0.20	0.16 - 0.24	0 - 1.00
106 - 110	37	0.30	0.06 - 0.54	0 - 4.17
111 - 115	19	0.09	0.01 - 0.17	0 - 0.77
Total	365			

adults. Although most individuals grow at or near the mean rate, yielding fairly compact 95% confidence intervals, some individuals grow at much slower or much faster rates. This great variation in growth rates superimposed on the variation in sizes of first-year turtles prevents the study of growth by tracing discrete size classes. Figure 6 shows the relationship between size and age indicated by growth rates. At the end of their first year, turtles average 48 mm, and one in its second year would grow 2.9 mm/month to 60 mm in early September. By then the turtle could be sexed and assigned to the appropriate growth rate for the remainder of September, and the following spring when it ordinarily would have attained a larger size class and slower growth rate. This procedure was extended to all growth rate categories determining confidence intervals and upper ranges on the growth curve (see Table 4). For some size classes minimum growth rate was zero preventing calculation of lower range size-age relationships.

Most males grow to maturity at 80 mm by the end of their fourth year (Fig. 6), as tentatively concluded by Webb (1962). Confidence limits indicate that some precocious individuals may mature by the end of their third year, and some late-maturing individuals may not mature until their fifth year. The upper ranges indicate that theoretically some fast-growing individuals might attain the size of maturity late in their second year or early in their third year. However, little confidence may be placed on this prediction because of its statistical nature and because it is unlikely that any one individual would grow at such an accelerated rate for an extended period. Growth rates are sensitive to seasonal and yearly trends as well as being sporadic in other, unexplained ways.

Fig. 6. The relationship of body size and age in male T. *muticus*. Dots are means; vertical lines are ranges; horizontal lines delimit 95% confidence limits.


LENGTH OF PLASTRON (mm)
100
80
60
40
0
4
8
12
16
AGE (years)

Mean size for mature males was 98.2 ± 0.24 mm (n = 1162); it would take approximately nine years to reach this size. Large males, those over 110 mm, probably grow at rates of about 0.10 mm per month, indicating that the largest male (123 mm) was about 48 years old. Because large individuals were rare, such turtles more likely represent those with accelerated growth rates. Rates ranged to 0.77 mm per month in the 111-115 mm class. Such growth would permit a turtle to reach 120 mm in as little as eight years. Although it is unlikely that any turtle would grow that fast for an extended period, large turtles probably are younger than 48 years. Webb (1962) indicated a maximum size of 140 mm in male _T. muticus_. Breckenridge (1955) determined that 10-year-old male _T. spiniferus_ would be approximately 6.25 inches (CL) in length and 15-year-olds would be about 6.75 inches. Converted to metric units and to probable plastral lengths from Webb's (1962) CL/PL ratio of 1.39 for _T. spiniferus_, Breckenridge's animals were 114.1 and 123.3 mm, respectively. In _T. muticus_, a smaller species, such age groups would have mean plastral lengths of 100.6 and 105.6 mm, respectively.

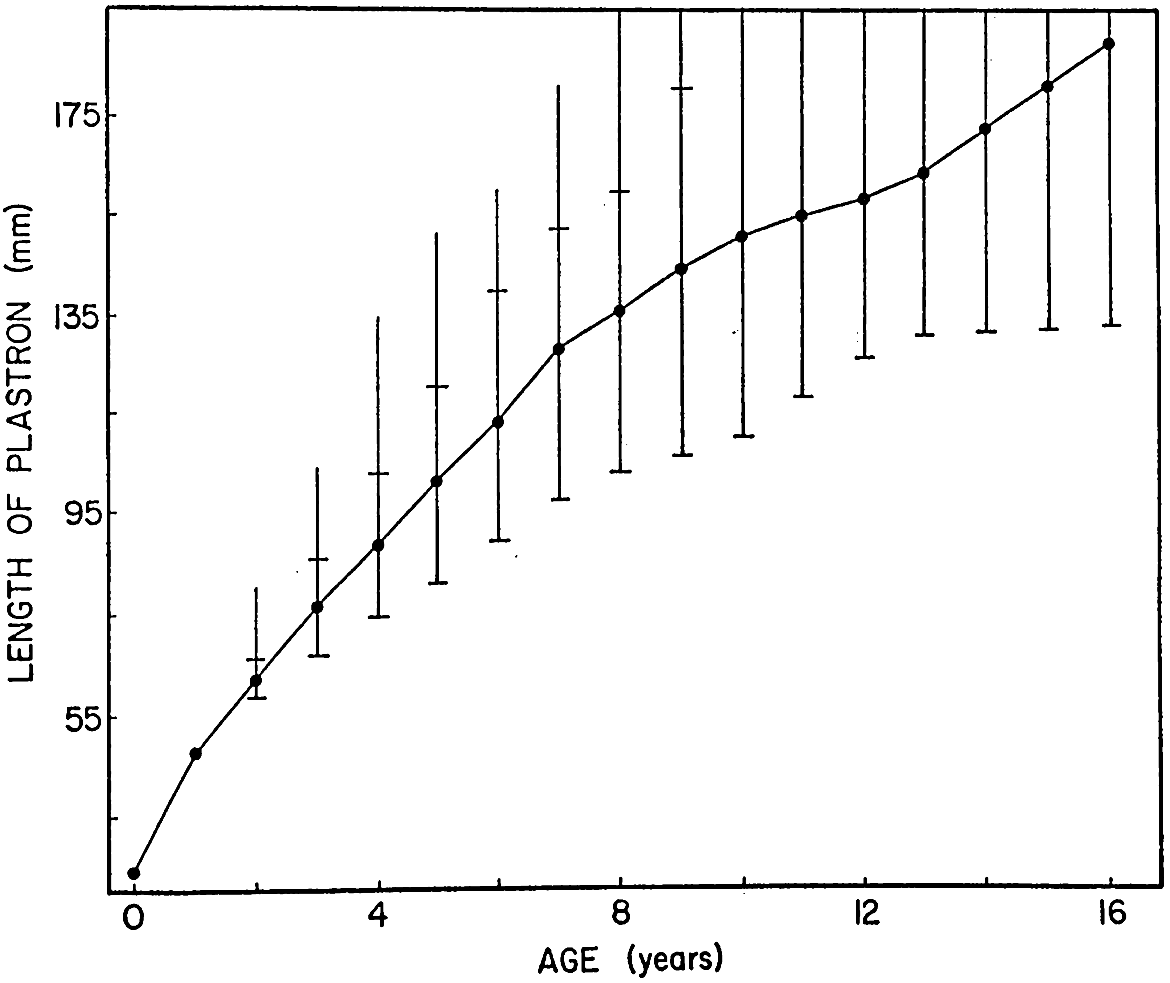
Growth of females. - Females seem to grow slightly faster than males (Table 5). Rate of growth declines as maturity is approached at about 135-140 mm, but large females continue to grow at rates greater than those in males. Confidence intervals are greater in females because of greater variation (10.86 mm per month maximum compared to 6.67 mm per month maximum in males), and to smaller sample sizes.

Females mature at about 140 mm, typically in their ninth year (Fig. 7). Confidence limits indicate that some individuals mature in their sixth year and ranges suggest that some might mature even in their

Table 5. Growth rate in female *T. muticus*.

PL	N	$\bar{Y}$	$\bar{Y} \pm 2$ S.E.	Range
61 - 70	7	2.79	1.61 - 3.97	0.33 - 5.00
71 - 80	12	3.20	1.50 - 4.90	0 - 10.86
81 - 90	14	2.23	1.39 - 3.07	0.44 - 5.00
91 - 100	12	2.75	1.61 - 3.89	0.36 - 6.76
101 - 110	10	2.09	0.79 - 3.39	0.24 - 5.56
111 - 120	9	2.46	1.68 - 3.24	1.14 - 5.20
121 - 130	4	3.98	1.44 - 6.52	1.64 - 7.33
131 - 140	4	1.37	0.09 - 2.65	0.17 - 3.10
141 - 150	4	1.70	0.36 - 3.04	0.46 - 3.60
151 - 160	4	0.70	-0.08 - 1.48	0 - 1.76
161 - 170	3	1.71	-0.73 - 4.15	0 - 4.07
Total	83			

Fig. 7. The relationship of body size and age in female T. *muticus*. Dots are means; vertical lines are ranges; horizontal lines delimit 95% confidence limits.


LENGTH OF PLASTRON (mm)
175
135
95
55
0
4
8
12
16
AGE (years)

fifth year, but little confidence may be placed in the extremes for reasons discussed above. The smallest mature female (131 mm) may have been in her sixth year. Mitsukuri (1905) wrote of the smaller T. sinensis: "In the sixth year they reach maturity and may begin to deposit eggs, although not fully vigorus till two or three years later." Webb (1962) predicted that some female T. muticus probably matured in their sixth year but most did not mature until their seventh year.

By applying Breckenridge's size-age analysis of T. spiniferus (1955; Fig. 4), Webb (1962) determined that females would mature in their 12th year, but he believed this to be an overestimate of the time required. My estimate of maturity in T. muticus (9 years) tends to bear out Breckenridge's estimate in a Minnesota population. T. spiniferus, a larger species, probably matures at a larger size, and attainment of maturity at larger body sizes characterizes northern populations in some turtles (e.g., Sternotherus; Tinkle, 1961).

Age-size relationships in three species of Trionyx are summarized in Table 6. T. sinensis is the smallest species (Ernst and Barbour, 1972) but it appears to grow as rapidly as the largest species, T. spiniferus, during the first five years. Inasmuch as Mitsukuri's (1905) study of T. sinensis was done in a commercial "turtle-farm" in which turtles were artificially fed, it seems reasonable to suggest that these turtles grew faster and perhaps matured earlier than they would have under natural conditions.

In my study mean size for mature females was 154.2 ± 0.66 mm (n = 173); a turtle of this size would be approximately 11 years old. The largest female was 186.0 mm in length and had grown from 163.0 mm in 5.5 growth months. Recorded lengths of 356 mm CL (Carr, 1952),

Table 6. Age-size relationships in three species of Trionyx: T. sinensis (Mitsukuri, 1905); T. spiniferus (Breckenridge, 1955; Fig. 4), and T. muticus (carapace length estimated from the average CL/PL ratio of 1.38 from Fitch and Plummer, 1975).

Age (years)	Length of Carapace (cm)		
	sinensis	spiniferus	muticus
0	2.7	3.3	3.3
1	4.5	7.0	6.6
2	10.5	10.1	8.6
3	12.5	13.0	10.6
4	16.5	15.2	12.3
5	17.5	17.1	14.1
6		19.7	15.6
8		20.3	18.8
10		25.4	20.8
12		27.3	21.8
14		28.6	23.7

345 mm CL (Ernst and Barbour, 1972), and of 215 mm PL (Webb, 1962) demonstrates that individuals do grow to sizes considerably greater than those I observed. The most probable age for the largest female is 16 years (Fig. 7), but confidence intervals for such large individuals are extremely wide. Breckenridge (1955) estimated that maximal-sized T. spiniferus (ca 450 mm CL) were about 53 years old.

Variation in growth rates. - The records of growth that were the bases for Tables 4 and 5 were obtained at various times of the year and spanned several years. Individual variation in growth rates is expressed in wide ranges and confidence intervals. Average growth rates also vary with ecological conditions. Rapid individual growth most often occurs in spurts. For example, one male in a size category usually characterized by slow growth (99 mm), grew only 1 mm in almost seven growth months, but thereafter he grew 8 mm in the next five growth months. Most such growth spurts could be attributed to either time-of-season differences or to yearly differences.

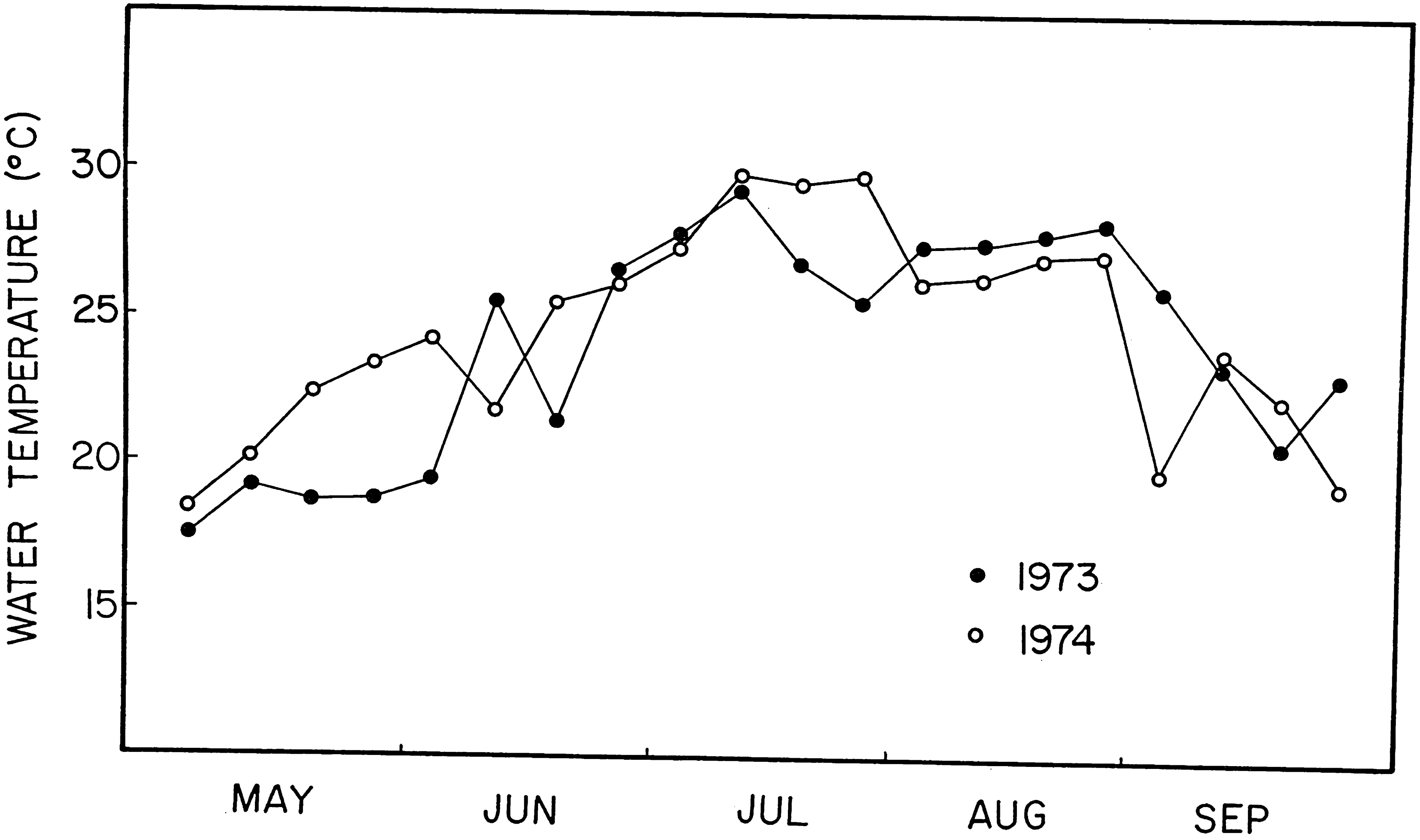
If yearly growth is divided into two 2.5 month segments (16 Jun. - 31 Aug. and 1 Sep. - 15 Jun.), growth rates are higher for mid-season than they are for early-late season (Table 7). The most obvious explanation for this difference is the higher average temperatures during the summer (Fig. 8) presumably involving maintainance of higher levels of metabolism.

In 1974, female samples grew more than twice as fast as in 1973, and males grew slightly faster in 1974 (Table 7). In the case of males the difference is not significant but the probability is only about 6 or 7% that it resulted solely from chance. These year-to-year differences in growth are not easily explained. Turtles became active much earlier in

Table 7. Variation in mean growth rate in *T. muticus*.

Sex	Time	Rate	N	Difference
Males	Early-late-season	0.56 ± 0.10	25	7.08 ($P<0.001$)
	Mid-season	2.73 ± 0.30	22	
Females	Early-late-season	0.57 ± 0.16	5	2.42 ($P<0.05$)
	Mid-season	3.68 ± 0.78	13	
Males	1973	2.17 ± 0.32	44	1.67 ($P<0.10$)
	1974	2.84 ± 0.65	19	
Females	1973	2.51 ± 0.34	20	4.47 ($P<0.001$)
	1974	5.57 ± 0.70	11	

Fig. 8. Mean weekly water temperatures for 1973 and 1974.


WATER TEMPERATURE (°C)
30
25
20
15
MAY
JUN
JUL
AUG
SEP
● 1973
○ 1974

1974 (Plummer, 1975b), and water temperatures were higher, especially in May and early June in 1974 (Fig. 8). Also in 1973 heavy precipitation with rapidly fluctuating high water levels contrasted with the relatively dry weather in 1974 with low, stable water levels. High water levels may scour the substrate and result in less available food and retarded growth. High water levels also limit basking activity by inundating preferred basking sites on sandbars and gentle slopes on mud banks.

Some authors have correlated rainfall and water levels with growth rates in turtles. Ernst (1971) found that drought reduced growth in Chrysemys picta through loss of habitat and loss of feeding patches of algae. Webb (1961) thought that water level might be a factor influencing growth in Pseudemys. Moll and Legler (1971) reported cyclic growth of Pseudemys scripta in the relatively constant temperature and photoperiod regimes of Panamá. Rapid growth was associated with the dry season and slower growth with the wet season. They suggested that turtles became inactive and did not feed during floods.

Cagle (1946) was one of the first to emphasize the extremely variable growth rates of individual turtles, geographical differences in growth rates, and the sensitivity of growth to ecological factors. Later studies by other investigators on additional species have borne out these characteristics of turtle growth. Gibbons and Tinkle (1969) demonstrated that in three populations in the same geographic area reproductive parameters may be strikingly different because of different growth patterns.

The trionychid turtles are one of the least known groups ecologically. Reproduction and growth is similar to that in other groups, but additional work is needed to compare variation in reproductive and growth parameters in time and in space (e.g., pond versus stream populations as well as among populations that are geographically remote).

SUMMARY

A population of Trionyx muticus in the Kansas River was studied from July 1972 to May 1975 by capture-mark-recapture. The major aspects of reproduction and growth were determined from 448 recaptures on 423 turtles and from 206 dissections. Males mature in their fourth year at a plastron length of 80 mm and females mature in their ninth year at 140 mm. Compared with males, mature females are larger, have shorter tails, and they develop distinctive blotched carapacial patterns. Testes are largest in late fall and smallest in early summer. Some ovarian follicles enlarge to preovulatory size in the fall in preparation for ovulation the following spring. Clutch size averages about 11 eggs and is related to body size. Number of clutches also is related to body size; females may lay two or more clutches per season. Clutch size was found to be smaller than those recorded in other studies of T. muticus in the same geographic area. Hatchlings have an average plastral length of 24.5 mm; this length is doubled by the end of their first year. Young males grow about 2 mm per month; with maturity growth abruptly decreases and becomes asymtotic. Females grow about 2-3 mm per month until maturity; growth rate then decreases but remains higher than in males. Average plastral length was 98.2 mm for mature males and 154.2 mm for mature females; these sizes were reached in 9 and 11 years, respectively. Growth in T. muticus is highly variable individually and is responsive to changes from month to month and year to year.

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IV. ASPECTS OF NESTING SUCCESS

INTRODUCTION

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; Burger, 1975, Wilbur, 1975). 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 unusually dry and water levels remained low and stable. These contrasting years offered opportunities to investigate the various aspects of nesting success reported herein.

MATERIALS AND METHODS

Field study. - The study area was a sandbar in the Kansas River, Douglas County, Kansas, which normally was exposed for a distance of

1-1.5 km depending on the water level (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 which were initially located near the water's edge. Occasionally tracks would lead to a turtle in some stage of the nesting process. When a nest was located its approximate distance from water, distance from vegetation, height above water, and longitudinal 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 number 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.

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 were also noted after water rises. The sandbar was staked in 100 m lengths for longitudinal measurement.

Experimental. - Seventy-five clutches were collected during June-July of 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 which had a temperature regime slightly higher than outdoor air temperatures.

Fifty-nine clutches collected over a 12-day span were used for submersion experiments. Each egg was randomly assigned to one of eight different boxes, two of which were controls for incubation without inundation; in six others eggs were immersed for periods of 12 hours to 15 days. Inundation in each box began at the same time. Because each egg was randomly assigned, each box held a random sample with regard to clutches and to degree of development (1-12 days). Sixteen other clutches were maintained as integral units and were incubated without submersion in boxes with individual eggs of a clutch in contact with each other. Contingency table analysis and the methods of Sokal and Rohlf (1965; p. 607) 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 (Figs. 1-2). Water level is not directly correlated with local rainfall; it is 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

Fig. 1. Rainfall at Lawrence, Kansas for 1973 and 1974. Each bar represents the mean of a three-day period. Source: U.S. Weather Bureau Climatological Data, Kansas Section.

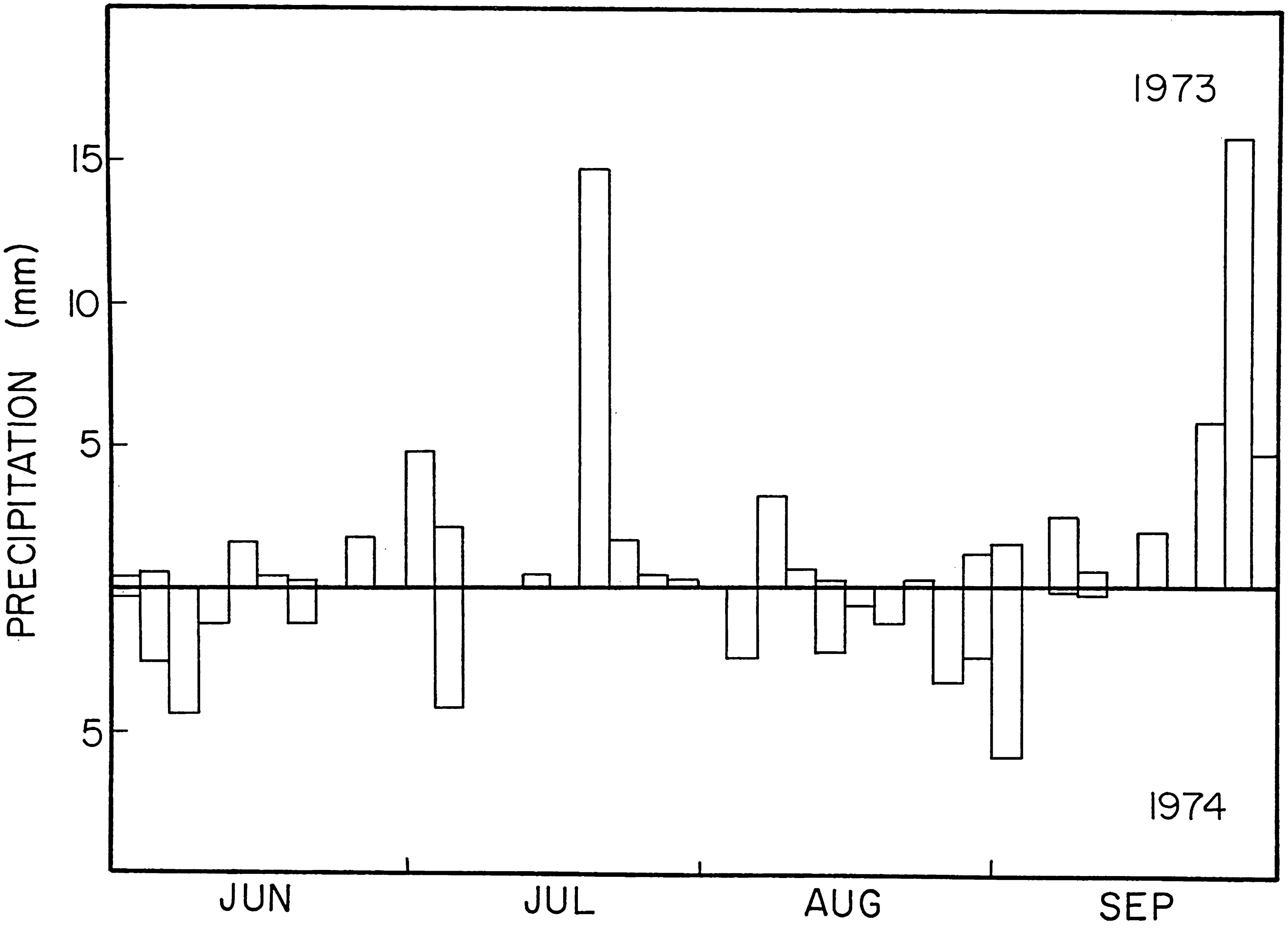
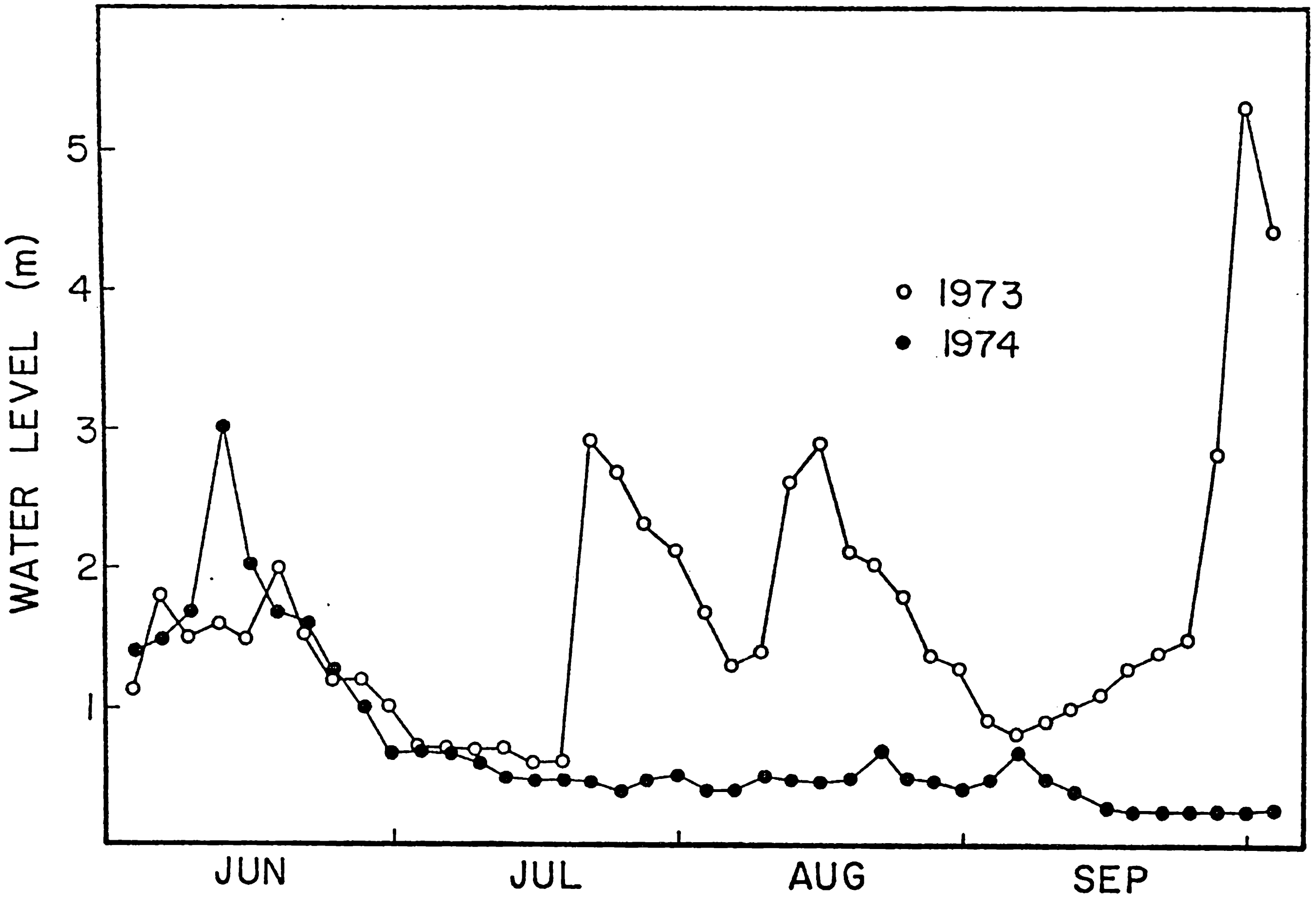

1973
1974
15
10
5
5
PRECIPITATION (mm)
JUN
JUL
AUG
SEP

Fig. 2. Water level of the Kansas River near study area for 1973 and 1974. Each point represents the mean for a three-day period.


WATER LEVEL (m)
5
4
3
2
1
○ 1973
● 1974
JUN
JUL
AUG
SEP

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 two years yielded 48 and 40 nests, respectively (excluding nests found by backtracking hatchlings on the open sandbar in 1974).

The first nest in 1973 was found on 18 June but nesting tracks were noted as early as 7 June. In 1974 the first nest and first nesting tracks both were recorded on 27 May. The last nest found immediately after construction was on 17 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. - Original observations on nesting behavior in *T. muticus* have been made by Muller (1921), Cahn (1937), Goldmsith (1944), and Fitch and Plummer (1975). New information offered in this paper includes observations on timing, and behavior after nest completion.

Nesting was concentrated in periods of sunny weather after periods of overcast or rainy days. Although the study area was searched every day during the nesting season, it would have been possible to overlook some nesting in heavy rain because of obliteration of tracks; however, nesting behavior usually was not seen for several overcast, rainless days before or after precipitation. Similar concentration of nesting activity in fair weather has been noted in *Malaclemys terrapin* (Burger and Montenecchi, 1975).

Most nesting females were found on the beach in late morning; some were found in early afternoon. Most fresh tracks of nesting turtles and the nests themselves also were found during these times. Nesting was not observed in late afternoon or evening even though the sandbar was searched during these times. Females may burrow immediately after completion of their nests. Their activity forms shallow troughs with the nest in one end and the female in the other. Most of the troughs were straight and less than 1 m long but one was about 4 m and followed a sinuous course. It was first thought that burrowing might be a means of avoiding high surface temperatures when nesting on a hot afternoon; however, instances were noted in the morning and some were seen on overcast days. Harper (1926) recorded the observations of A. Chesser who noted that nesting softshells (probably _T. ferox_) often burrow before returning to water.

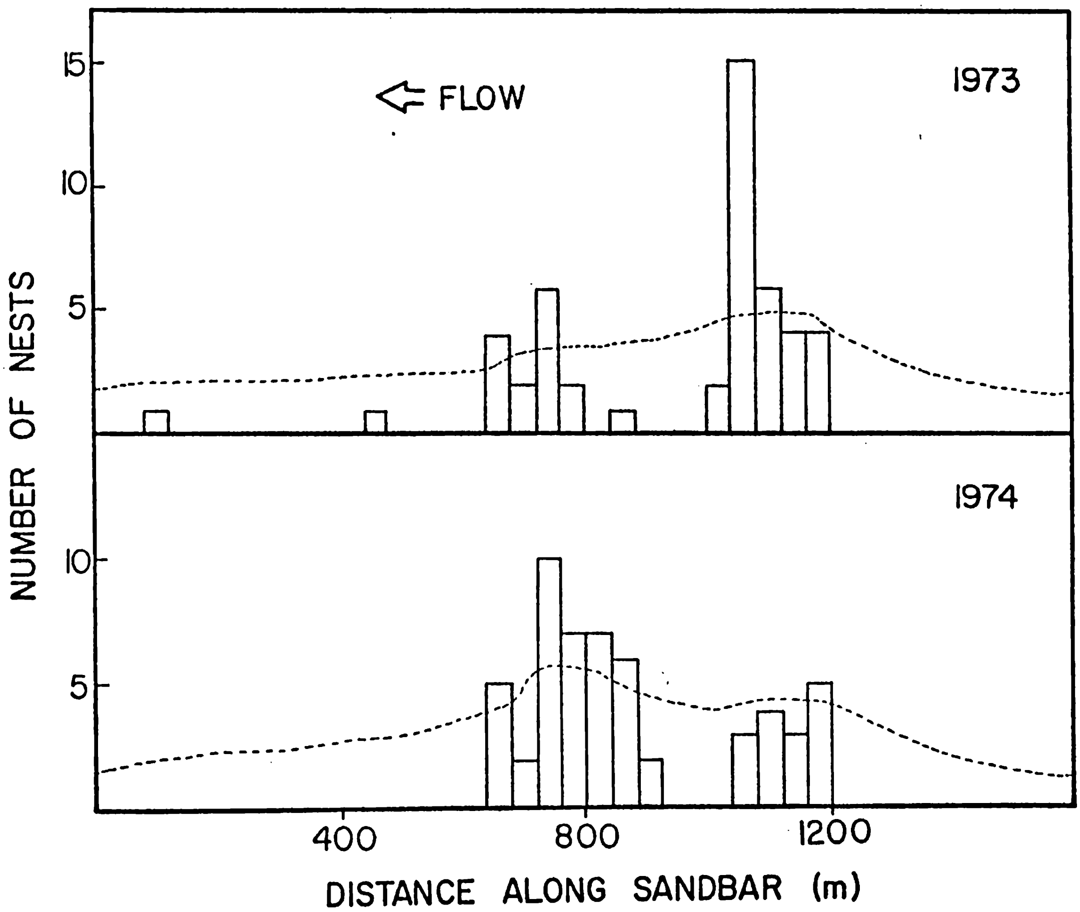
Nest site preference. - Most nests were constructed on open sandbars free of vegetation, but in certain areas subsequent growth of annual vegetation shaded the nests and infested them with root growth. During periods of high water turtles nested in small patches of sand among dense, permanent vegetation (primarily saplings of cottonwood, _Populus deltoides_, and sandbar willow, _Salix interior_). Most nests were located 10-90 m from the permanent vegetation line; however, when water levels were low, a female emerging near the widest portion of the sandbar might nest several hundred meters from the vegetation. Similar observations on nest site preferences have been made by Goldsmith (1944), Anderson (1958), Webb (1962; pl. 50), and Fitch and Plummer (1975). In 1973 a large sandbar 6 km downstream from the study area had a higher concentration of nests that 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.

Constant currents generally mold sandbars with extensive flat areas that gradually slope up to a ridge and then abruptly slope down to another flat. The resultant one or more high ridges are oriented at an angle to the shoreline. Nests are clumped at the highest points (ridges) on the lateral profile of the sandbar (Fig. 3). Severe flooding during the winter of 1973-1974 shifted the main high ridge of the sandbar downstream about 400 m. A corresponding shift of nesting density followed in 1974.

In Figure 4 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 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.

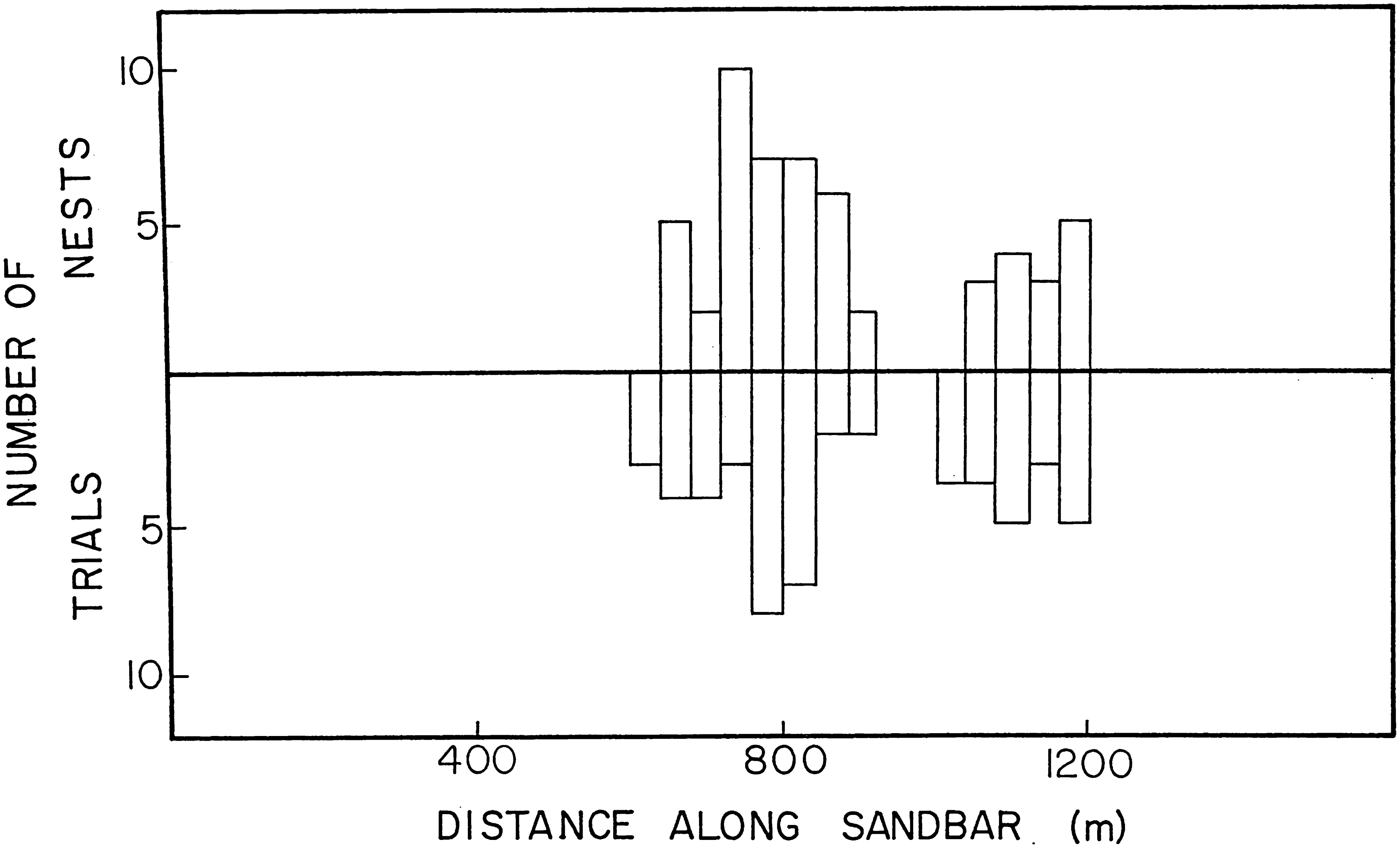
Fate of nests. - A clutch laid is subject to various hazards -- predation, erosion and destruction by rainwater if laid on a steep slope, washing out and destruction by currents with rapidly rising river water, infertility, attack by fungus, infestation with root growth, and inundation for varying lengths of time sufficient 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. Canids predated on seven nests in 1973 and on two nests in 1974. Considerable intervals (1-7 weeks) elapsed between oviposition and predation on

Fig. 3. Distribution of nests at the study area for 1973 and 1974. Dashed line represents simplified longitudinal profile of sandbar.



FLOW
1973
1974
NUMBER OF NESTS
15
10
5
10
5
400
800
1200
DISTANCE ALONG SANDBAR (m)

Fig. 4. Distribution of nests at study area in relation to distribution of emergence points of large females which wandered on the sandbar but did not oviposit in 1974.


NUMBER OF
NESTS
TRIALS
10
5
5
10
400
800
1200
DISTANCE ALONG SANDBAR (m)

these viable clutches. Moll and Legler (1971) found through experimentation that predators on nests of Pseudemys scripta usually took eggs soon after oviposition when olfactory cues (from urine and eggs) were strongest. 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 throughout the seasons and were subject to different fates as summarized in Table 1. A major difference in survival between the two years resulted from long periods of inundation in 1973. Most of the nests were inundated for 2-12 days after the water level rose on 20 July (see Fig. 2). Other periods of inundation began on 9 August and 24 September. Apparently periods of inundation of only a few days damage or destroy T. muticus eggs; this conclusion was substantiated by laboratory experiments. In 1973 seven eggs hatched from a clutch of 15 which was inundated about three days, and two eggs hatched from a clutch of nine which was not inundated. In 1974, only five intact nests were inundated for about 24 hours; 52% of the eggs in these five nests eventually hatched. This percentage is not statistically different from the normal percent of successful eggs (see Table 2).

Clutches deposited in sand were largely free from the deleterious effects imposed by media containing much silt -- increased water retention after inundation and/or precipitation and damage from root and fungal growth. In general, most successful nests were laid in sandy media high enough so that inundation did not occur.

Experimental. - In incubation experiments the effects on the eggs of handling, of light-dark regimes, and of relatively more constant temperature and moisture regimes should caution the direct comparison to field results. Some eggs apparently absorbed sufficient moisture to enlarge

Table 1. Comparison of the fates of intact nests for two years.

Length of inundation (days)		No. nests	No. eggs	No. eggs hatch	Percent hatch
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

Table 2. Comparison of various parameters for laboratory and field clutches in 1974.

	No. clutches	No. eggs	Percent hatch	Percent no development	Percent died in shell	Mean incubation or emergence
Laboratory	16	154	60.4	31.8	7.8	49 ± 2.4
Field	32	319	63.3	26.0	10.7	68 ± 1.4

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 immersed the water was not changed until treatments ended. Metabolic heat from incubating turtle eggs may raise nest temperature several degrees over ambient temperature (Bustard and Greenham, 1968; Burger, 1975). In laboratory containers metabolism would raise the temperature of the water and deplete its oxygen content, but in natural nests rising water level usually is associated with slightly lower temperatures and higher oxygen 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 reopening nests in order to minimize disturbance. After hatching, the young may remain in the nest several days.

No significant difference from the control groups in percentage of eggs hatched occurs until eggs are submerged for two days (Table 3). The decline from the 12 hour group to the 24 hour group is not significant nor is that from the 24 hour group to the 2 day group but the probability is low ($P<0.07$) that this decline occurred by chance alone. Chance of surviving sfter submersion beyond 24 hours is less than with no submersion; increasing lengths of submersion result in decreasing survivorship; and after submersion greater than four days there is little chance of surviving.

Table 3. Results of submersion experiments. Vertical lines are maximum non-significant subsets.

Treatment	No. eggs	No. hatch	Percent hatch
Control	87	40	46.0
Control	86	33	38.4
12 hrs.	83	32	38.6
24 hrs.	85	29	34.1
2 days	86	16	18.6
4 days	82	10	12.2
8 days	84	3*	3.6
15 days	83	0	0

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

The difference in percentage of eggs that 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. The only difference in treatment was that the laboratory control clutches were maintained as integral units, whereas in the controls of the experiments the eggs were freely mixed and randomly assigned in different boxes. Perhaps activity of embryonic turtles of the same developmental stage produces mutual social stimuli affecting development in a given clutch. Audible sound has been detected in the latter stages of development in Chelonia (Balazs and Ross, 1974). Lee (1968) suggested that embryonic growth in Alligator might be stimulated by communication among siblings. This probably is not a significant factor in the present case, however, because most eggs which failed to hatch in the experimental controls apparently were infertile.

Hatching and emergence. - Carr and Hirth (1961) found that emergence success in Chelonia nests depended on the number of hatchlings; greater numbers of them apparently resulted in more social stimulation which promoted more vigorous upward digging by each, thereby increasing their success in escaping from the nest. In T. muticus the relationship between number of turtles hatched in a nest and number of hatchlings subsequently emerged is significant for the first eight categories (Table 4). There seems to be a minimum number at which greatest success is attained. All nests which had seven or more hatchlings had 90% or greater emergence, whereas in nests with fewer than five hatchlings there was 50% or less emergence. Those nests with 5 or 6 hatchlings seem to be moderately successful in emergence. An alternate explanation would be that nests having small numbers of eggs hatching represent clutches of

Table 4. Relationship between number of eggs hatched and emergence in intact nests in the field. Kendall coefficient of rank correlation for first eight categories (N) = 40 ($P<0.05$).

Turtles hatched in nest (N)	Nests (N)	Hatchlings emerging (N)	Percent emergence
2	2	2	50.0
3	2	0	0
4	3	4	33.0
5	5	19	76.0
6	7	36	85.7
7	5	35	100.0
8	5	37	92.5
9	6	54	100.0
10	8	79	98.8
11	6	64	97.0
12	3	34	94.2
13	1	13	100.0
14	1	14	100.0
15	1	15	100.0

less viable eggs and subsequent hatchlings incapable of digging vigorously. Emergence behavior in T. muticus probably is similar to that of Chelonia. Small depressions in the surface of the sand were seen in 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 eggs shells beneath. These turtles apparently were prepared for a mass emergence as occurs in Chelonia (Carr and Hirth, 1961).

Hatchlings emerge and leave 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 leave nests and move away from the water toward the permanent vegetation. Most eventually turned to the 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 two years was the length of time in which eggs were subjected to inundation. Eggs can withstand short periods on inundation without deleterious effects but inundation longer than two days significantly decreases chances of normal development. Sandbars used for egg deposition represent unstable environments with various potential hazards. Water levels may fluctuate rapidly over a range of several meters depending on rainfall and man-controlled regulation of output from dams. Nests situated at the highest points on sandbars have the greatest chances of survival. It is adaptive to nest in permanent vegetation when water levels are high despite the risks of root damage and shading. 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 an evolutionary analysis of *Chrysemys picta*, Wilbur (1975) concluded that its life history parameters were attuned to an extremely unpredictable chance of reproductive success, and this probably is true in general for turtle life histories including that of *T. muticus*; they are notably uniform and conservative.

SUMMARY

Nesting success of *Trionyx muticus* was studied 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 are preferred nesting sites; apparently females recognize these areas from the water. Predation on nests was low. The major cause of egg mortality was submersion produced by extended rises in water level; laboratory experiments suggest that egg viability is decreased when submersion lasts for more than one day. Nesting success was lower in 1973, an unusually wet season, than in 1974 which was unusually dry. Evidence indicates that there must be a minimum number of hatchlings in a nest to insure escape from the nest.

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