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Activity, Habitat and Population Structure in the Turtle, *Trionyx muticus*

MICHAEL V. PLUMMER

A riverine population of *Trionyx muticus* was studied for 3 years by capture-mark-recapture. These turtles were most active from May through September. Trapping success was affected by changes in water level, and a midsummer period of inactivity was associated with low, stable water levels and high water temperatures. Males preferred areas with emergent sandbars but females preferred deeper, more open water except during the nesting season when they moved into shallow water adjacent to 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 1900 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 temporary emigration and immigration.

FRESHWATER turtles often occur in discrete populations in partially isolated bodies of water (Cagle, 1944; Sexton, 1959; Gibbons, 1968; Wilbur, 1975), allowing study of relatively closed systems. 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 *Chrysemys* occupied well defined segments of streams. Moll and Legler (1971) found that some adult *Chrysemys* 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. Plummer and Shirer (1975) demonstrated that individuals in river populations of *Trionyx muticus* had restricted home ranges but these areas might be shifted frequently and there was little tendency for the turtles to return to them after being artificially displaced. Plummer and Shirer suggested 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 general view that turtles show lasting fidelity to a restricted area (Porter, 1972: 474-475).

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 trionyichids, remains poorly known. The population on which this report is based has been studied previously. Webb (1962) listed stomach contents of several individuals. Fitch and Plummer (1975) presented a preliminary ecological report. Plummer and Shirer (1975), and Plummer (1976, 1977 a,b) reported on movement patterns, nesting success, courtship and mating, and reproduction and growth, respectively. This paper describes activity, habitat preferences and some aspects of population structure.

METHODS

Turtles were collected from July 1972 through May 1975 from a 14 km section of the Kansas River downstream from the Bowersock Dam at Lawrence, Douglas County, Kansas. Traps, constructed of 2.5 cm mesh chicken wire, measured 20H × 50W × 60L cm and had a single funnel opening (2 × 50 cm). Traps were set in shallow water (<30 cm) and were checked and rebaited daily from May to September and about every other day earlier or later in the season. Thus, trapping effort remained nearly constant for most of the season. Traps were

baited with fresh chopped fish or commercial dog food (Friskies Sauce Cubes) with equal success. Turtles did not enter unbaited traps, or those with bait more than 1–2 days old. Hand collecting involved locating turtles beneath the sand by probing with a blunt metal rod. Probing along edges of emergent sandbars was productive primarily in the latter part of 1974 when low and stable water levels yielded relatively clear water.

For each turtle the length of the plastron (PL) was measured midventrally with a plastic ruler to the nearest millimeter from the posterior edge to the anterior edge, including the marginal cartilaginous portion. Each turtle was uniquely marked with a series of triangular notches cut with a penknife at different positions in the edge of the carapace, and released. 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 and maintained every 100 m. Additional collecting was done at locations extending 6 km up- and downstream from the main study area. A water level gauge and a Taylor maximum-minimum thermometer were installed 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 was measured between lines connecting the outermost claw marks on each side. All statistical tests are those of Sokal and Rohlf (1969).

RESULTS

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 inundated when floods occurred. It had greater concentrations of turtles than areas adjoining it upstream and downstream.

Characteristics of the Kansas R., both within the main study area and farther upstream and downstream are important for an understanding of the turtles' population structure. Within the 14 km section the river at highwater varied from 150–450 m in width and its lowest stages from 80–250 m. 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, turtles moving downstream could cross the dam. Consequently, the population of the main study area was diluted by immigrants from both ends. Approximately 2,300 captures of 1,500 turtles were made in the 1.5 km main study area and approximately 3,700 captures of 2,700 turtles were made in the 14 km section. Aerial and/or habitat photographs of these areas were presented in Plummer and Shirer (1975) and in Fitch and Plummer (1975), respectively.

Activity.—Turtles were first noted between 30 March and 21 April (water temperatures 13.5–15.0 C) and were last noted between 14 and 26 October (water temperatures 19.0–20.0 C). Activity toward the beginning and end of the seasons was sporadic and strongly weather-dependent. Activity began early in 1974 when extended warm, clear weather caused water temperatures to rise, but sustained activity did not begin until late April. Seventeen turtles were captured on 30 March but only 4 more were captured during the next 3 weeks. Likewise, sustained activity in the fall ceased sooner than the extreme records indicate. The normal activity season extended from May through September. Figure 1 shows the frequency distribution of combined captures for 2 field seasons. The distribution is bimodal with a decrease in captures during mid-summer suggesting lower activity at that time. In spring females were first collected later than males (Fig. 1), and adult females were collected later than subadults. Only 8 adult females were captured before June in 3 seasons of intensive collecting. However, adults occasionally were seen courting and basking.

In 1973 abundant rainfall throughout the year caused high and fluctuating water levels, whereas little precipitation and low, stable water levels characterized 1974. Factors which might affect activity were investigated using trapping rates as a measure of activity (Fig. 2). In 1973 rates were bimodal and similar to distribution of captures. In 1974 rates were unimodal with a peak in mid-June. Trapping rate shows a remarkable correlation with water level, usually increasing following a rise in level and decreasing following a drop. The association is

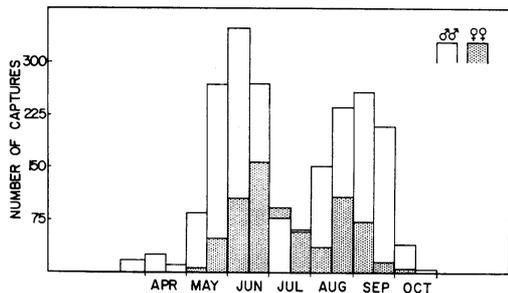


Fig. 1. Seasonal distribution of captures for 1973-1974.

TABLE 1. PERCENT OF DAILY OBSERVATIONS OF MARKED TURTLES THAT WERE LOCATED 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)

extremely close in 1973 except for week 18 where the pattern is reversed. In 1974 the association is extremely close after week 7. The 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.

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

Plummer and Shirer (1975) relocated 28 *T. muticus* tagged with radio transmitters 741 times. I categorized the habitat at each of these

relocations and tallied them for comparison (Table 1). Males spent more time in emergent sandbar habitat than did females ($t = 6.15$; $P < 0.001$). Subadult females appear more inclined to sandbars than adult females, but less inclined than males. These data agree with daily observations as females were not often captured on sandbars except during the nesting season. Although males occurred in virtually every habitat in the river, they were most abundant near sandbars. Basking females were not observed so frequently and most of them were on steep mud banks near deep water.

Sandbars contain several microhabitats which are not equally utilized by turtles. Sandbars often have 1 or more ridges which extend far out into the river, and abruptly slope into water at the lee edge. There may be small inlets of quiet shallow water in these areas which are utilized heavily by turtles for aquatic basking late in the season. On 26 September 1974, in 1 such area approximately 4×12 m, 73 burrowed turtles were captured by hand in about 30 min. On another occasion, in an area ap-

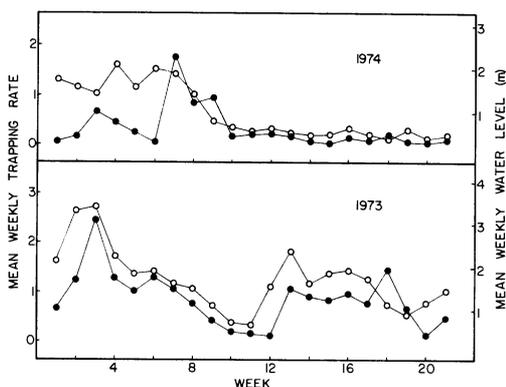


Fig. 2. The relationship of trapping rate (no. turtles/trap-day) to water level from May-September for 2 years. Closed circles are trapping rates; open circles are water levels.

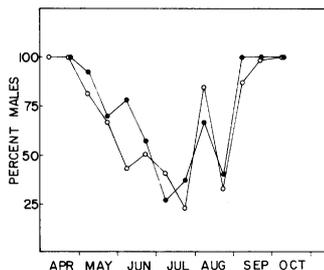


Fig. 3. The relationship of sex ratio to time of season in 1974. Closed circles are turtles captured in traps; open circles are hand collected turtles.

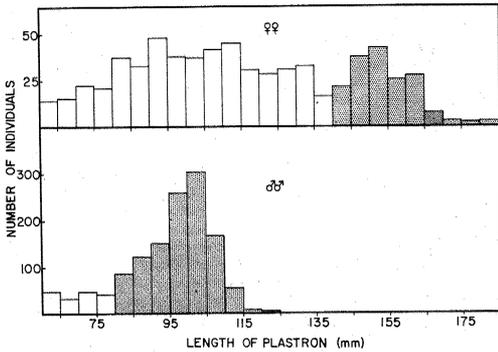


Fig. 4. Distribution of body sizes for captured turtles. Stippled bars represent mature turtles.

proximately 1.5×10 m on a sandbar about 35 m in length and 1.5 km distant from the next nearest sandbar, 48 turtles were captured on 1 day, and 64 on the succeeding day. Only 2 of the 64 turtles were recaptures from the first day. Water temperature of this area was 25.5 C whereas temperature of the main stream was 19 C.

Sex ratio and size structure.—I recorded 1,162 adult males and 172 adult females, yielding a sex ratio of 6.8:1. The sex ratio of all turtles 60 mm or larger was 1.98 ♂♂:1 ♀. However, this ratio varied seasonally (Fig. 3). Sex ratio was independent of collecting technique (Fig. 3). Ratios derived from each method deviated from each other only in May and early June when females were captured on sandbars in search of nesting sites, and when males were attracted to

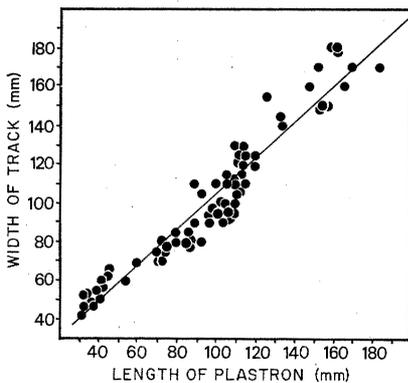


Fig. 5. The relationship of width of track to length of plastron in 73 turtles. The regression equation is $\hat{Y} = 11.78 \pm 0.93x$ ($P < 0.001$).

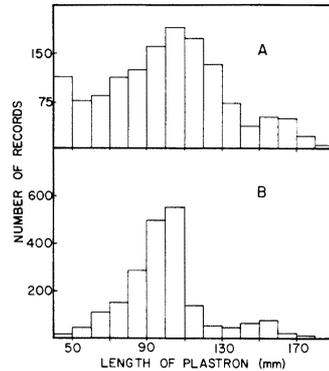


Fig. 6. A. Distribution of body sizes according to beach tracks (measurements taken throughout the season). B. Distribution of body sizes according to captures.

females in traps. Unbaited traps containing females attracted large numbers of males. On 10 May 1975, 36 males were found in 1 trap with 1 adult and 1 subadult female. Catches of 5–15 turtles in a single trap were not uncommon in spring.

Figure 4 shows the distribution of sizes in the population. Eighty-two percent of the males were mature, but only 25% of the females were mature. Thirty-seven percent of the total sample were immature turtles.

A close relationship exists between width of track and length of plastron (Fig. 5). Each track made by captured and released turtles was measured in moist sand near the water's edge. Figure 6 compares size structure of the popula-

TABLE 2. WEEKLY POPULATION SIZE ESTIMATES (JOLLY, 1965) OF MALES FOR THE LATTER PART OF THE 1973 FIELD SEASON.

Week	Proportion of recaptures	Marked animals at large	Pop. size ± 2 SE
1	0.42	822	1,943 \pm 1,797
2	0.29	332	1,160 \pm 959
3	0.56	281	506 \pm 212
4	0.36	238	655 \pm 413
5	0.30	476	1,571 \pm 803
6	0.35	441	1,259 \pm 746
7	0.47	486	1,024 \pm 421
8	0.50	441	882 \pm 529
9	0.05	495	9,405 \pm 9,397
10	0.45	1,029	2,287 \pm 2,671

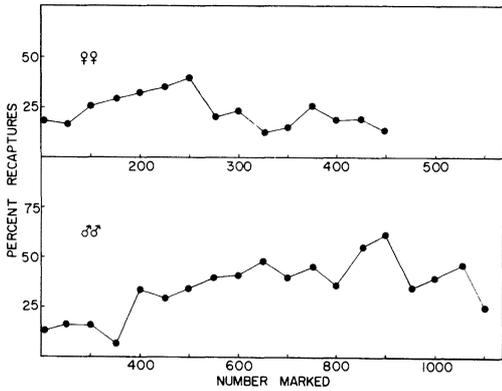


Fig. 7. The relationship of percent of recaptures to cumulative number of turtles marked.

tion according to captures to that according to beach tracks (excluding hatchlings).

Population size and spatial characteristics.—Jolly's (1965) method was used to estimate the abundance of turtles on the main study area. Weekly estimates of proportion of recaptures, marked animals at large, and population size, were determined separately for males and females. All were characterized by great variability. In males (Table 2) changes as great as a 10× increase in population size were indicated during a single week, and larger changes were found in females.

Contrary to expectations, proportion of recaptures did not continue to increase as more turtles were marked (Fig. 7). Maximum ratios of recaptures to captures of unmarked individuals were reached quickly and hovered just under 0.50 for males, and near 0.25 for females.

TABLE 3. NUMBER OF RECAPTURES OF ALL TURTLES FITTED TO A POISSON DISTRIBUTION. $\bar{Y} = 0.514$; $G = 229.77$ ($P < 0.001$). Source: Sokal and Rohlf (1969).

Number of recaptures	Observed	Expected
0	1,045	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

TABLE 4. THE CORRELATION BETWEEN TIME AND 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: $r = 0.91$ ($P < 0.01$). Females: $r = 0.78$ ($P < 0.01$). Numbers in parentheses are sample sizes. Source: Sokal and Rohlf (1969; p. 533–538).

	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)

Table 3 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. When distributions of recaptures of males, adult females, and subadult females are analyzed separately, the results are similar in each case to Table 3, but means are lower in females than in males.

Table 4 demonstrates the correlation between elapsed time after marking and proportion of turtles marked in a given period which were later recaptured. Trapping records included individuals that originally had been caught on the main study area, were recaptured several

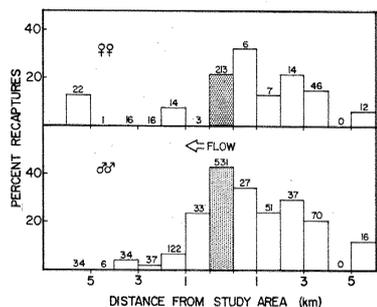


Fig. 8. Percent of turtles captured at various distances from the main study area which had been previously marked on the main study area. Stippled bars represent main study area; numbers above each bar are sample sizes. Double line at right represents Bowersock Dam—an absolute barrier to upstream movement.

km distant, and were later recaptured again on the main study area.

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.

DISCUSSION

The activity season of *T. muticus* is similar in length to that of *T. spiniferous* at similar latitudes (Webb, 1962). In each year trap captures began later in spring and ended earlier in fall than hand captures and sight records. This disparity suggests that activity occurs before feeding begins early in the season and after feeding ends late in the season. However, 1 of 2 males hand captured on 30 March 1974 had fresh food in its stomach, and 3 males captured on 9 April 1974 contained food. Four of 5 males collected in late September 1973 contained food but 2 others captured on 7 October and 2 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.

Differences in water level per se probably do not affect the number of turtles entering traps. However, low, stable water levels were associated with higher water temperatures, lower current velocities, lower turbidity, and algal blooms. High water and fast current undoubtedly scoured the bottom and reduced food availability. In 1973 range of water levels was about 9 m. Perhaps baited traps were especially attractive when other food sources were unavailable during high water, or perhaps the swift current dispersed the bait scent more widely and rapidly, thus attracting more turtles. Webb (1962) mentioned that a commercial fisherman in Mississippi captured numerous soft-shells in unbaited traps when the river was receding from heavy rains.

The difference in habitats preferred by males and females (Table 1) is supported by other data. Females frequently were encrusted with epizoaic colonial protozoa [primarily forms of *Anarma*, *Epistylis*, *Opercularia*, *Rhabdostyla* and *Tokophrya* (Bovee, 1974)], whereas males seldom had such symbionts. The colonies occurred on the dorsal and ventral aspects of the posterior carapace; perhaps protozoa were worn off the anterior portions by burrowing. Most females had at least light growths but some individuals were heavily encrusted with thick, feath-

ery colonies. The difference in occurrence of epizoaic between the sexes suggests that males live in warmer, shallower water and bask frequently (which would discourage growth of protozoa because of the frequent desiccation and/or temperature extremes), while females live in deeper, cooler water and bask less. Plummer and Shirer (1975) found that males and subadult females could be followed near sandbars by tagging with balloons—a technique unsuccessful with adult females because of extensive movements. They found that signals from radio-tagged females frequently were lost in deep water whereas those of males were almost always audible because they stayed in shallower water near sandbars. Late in the season turtles normally staying in deep water in preparation for hibernation probably seek microhabitats which allow them to raise their body temperatures on warm, sunny fall days. Turtles rarely bask on shore during these seasonal extremes and the warm inlets of water near sandbar points are quickly accessible from deep water.

Sex ratios of juvenile turtles are generally equal but those of adults tend to deviate from parity with females often predominating. Gibbons (1970) concluded that data were insufficient to demonstrate that turtles have unequal sex ratios. Gibbons thought that errors in sexing or selective sampling caused by behavioral differences between the sexes were present in most studies.

Male *T. muticus* mature at a plastral length of 80 mm and females mature at 140 mm (Plummer, 1977b). The largest male was 121 mm; thus adult males and adult females fall into discrete size groups. The cloaca lies anterior to the posterior edge of the carapace in subadult females, whereas adult males of this size have the cloaca lying at or beyond the edge (Plummer, 1977b). These secondary sexual characteristics made errors in sexing turtles improbable. The reason for the imbalanced sex ratio is not entirely clear, but sampling was successful along sandbars in habitat preferred by males and was unsuccessful in deeper water where females preferred to stay. Movement of females into shallow water along sandbars during the nesting season and afterwards rendered them more susceptible to capture and therefore reduced male preponderance in the sex ratio. The attraction of males into traps containing females would also favor a preponderance of males. Another possible cause of male preponderance could be that males mature about 5

years earlier than do females (Plummer, 1977b); this would be important in biasing the sex ratio of adults in a young population. There is no reason to believe that mortality was higher in females. Only 15 males and 6 females were found dead during the course of my study and the causes of death in these animals were unknown. Fishermen catch softshells on their lines and especially in their nets. During harsh winters softshells are at the mercy of large moving ice packs that scour the bottom where turtles hibernate, but these sources of mortality probably are not sex-selective.

My estimate of 37% immature turtles in the population agrees with the generally high proportion of immatures in populations of aquatic species (Moll and Legler, 1971). However, my figure may be too high (assuming immature turtles were correctly represented) because adult females probably were not captured in numbers representative of their real abundance.

There are some differences when size distribution according to captures is compared to that according to beach tracks (Fig. 6). 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 occupied different habitats than those where traps were located. The probability of locating smaller turtles by probing was lower because of the smaller target area. The population probably includes a larger proportion of small turtles than capture records indicate. In B, the proportion of turtles 90–110 mm is greater and this probably is more accurate than beach tracks indicate. Basking was concentrated at certain sites, and mature males were prevalent judging from study of basking groups through binoculars. Because of the concentrated aggregations, the number of individuals represented by the masses of tracks at any given site was difficult to determine. In making counts I was conservative to avoid duplications, and probably underestimated the numbers of individuals. Probably an important reason why A is symmetrical is that track widths for individuals of a given size are normally distributed resulting in normally distributed predictions of plastron lengths.

Large fluctuations in population size estimates were not expected in such long lived animals. The fluctuations were puzzling since field observations suggested a more or less constant number of turtles. Some insight may be gained by examining the underlying assumptions of Jolly's method.

Models for estimating population size based

on capture-mark-recapture are most reliable if a high proportion of the animals are marked. This was not true in the present study (Fig. 7). Because proportion of recaptures did not continue to increase, the population was continually being diluted with respect to marked individuals. Five of 15 males found dead and 1 of 6 females found dead were marked. These proportions were less than proportions recaptured; therefore higher mortality on marked turtles apparently did not cause dilution. Recruitment by natality in this slow maturing, seasonally-breeding species could not have caused the continuous, high level dilution. Another possibility is that I only sampled a subset of a larger population. If individuals moved freely over a larger area, then outward flow of marked turtles and influx of unmarked turtles could have caused continuous 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.

The Jolly model allows for movement into and out of the sampled area but requires that such movement be permanent. The method assumes 3 possibilities for an individual present at time i in the $i+1$ th sample: It may be recaptured; it may still be 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 which would cause unequal probability of capture and subsequent fluctuations in marked animals at large and proportion of recaptures. Because population size is obtained by dividing number of marked animals at large by proportion of recaptures, the quotient would be quite variable.

Table 3 demonstrates that probability of capture was not equal once a turtle was marked. The larger than expected zero class probably represents transients or highly mobile turtles which had a low probability of recapture. Records of 1 or 2 recaptures probably were influenced by the same phenomenon, i.e., most turtles moved freely over large areas yielding smaller than expected numbers of turtles which were recaptured 1 or 2 times. Classes with 3 or more recaptures have more individuals than expected; these were unusually sedentary males. For example, 2 males were each recaptured 9 times in the main study area over periods of 4 and 9 months, respectively.

The correlation between elapsed time after

marking and proportion of recaptures suggests that turtles do return after leaving the area sampled, supporting the thesis that there was relatively free movement of the population within a more extensive area.

Individuals are capable of frequent and long movements (Plummer and Shirer, 1975). The results of the Jolly analysis and the low recapture rates suggests that a substantial proportion of the population engages in such movement. Remarkably high proportions of recaptures were found at distances up to 6 km from the main study area (Fig. 8). Contingency table analysis (Sokal and Rohlf, 1969) 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 to 3 km upstream from the main study area were not significantly different from the proportions within the main study area. The greater movement of females influences these results so that for females there is greater variation in Jolly estimates, and lower recapture rates. The concentration of recapture records upstream from the main study area probably 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 4 km downstream a few days after release. Passive dispersal probably is important in their dynamics.

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. 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. Because previous studies of freshwater turtles indicated that individuals were localized and that populations were well-defined, I assumed at the onset that the turtles of the main study area could be regarded as a discrete population with emigration and immigration constituting relatively minor factors in its dynamics. However, as the study pro-

gressed, my assumption was suspect and collecting up- and downstream from the main study area was increased during the latter part of 1974 and in 1975.

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 *Chrysemys 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.

Differences between pond and stream environments might be reflected in structure of their turtle populations. In streams lack of physical barriers and the potential 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 case in riverine populations of *T. muticus*. It now is clear that my "population" was not a natural unit; the real population extended over several km and apparently was not subdivided. Over 200 turtles were collected, primarily at a sandbar 6 km downstream from the main study area, and dissected for reproductive data (Plummer, 1977b). Some of these turtles probably were integral members of the population sampled at the main study area. These individuals were included in size structure analyses (Figs. 4, 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 may be subject to question. These and other implications are discussed by Ehrlich et al. (1975).

An accurate estimate of the number of turtles on the main study area is difficult to ascertain.

Direct counts even for small areas were unfeasible and indices based on capture-mark-recapture were biased because of the movement patterns. However, 2 different approaches yield figures of similar magnitude and serve to give a composite estimate of the abundance of turtles greater than 60 mm in length.

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 marked animals at large would fluctuate greatly over short time spans due to leakage; however, if the number of marked animals at large was averaged over longer periods, return of some marked animals that had left the sampling area would tend to compensate for leakage. Averages for the combined weekly estimates in *Trionyx* indicated 1,338 males and 463 females. Hayne (1949) reasoned that the shorter the period between marking and resampling, the less would be the effect of movement into and out of the population. His method estimates 1,610 males and 641 females if the entire season of 1973 is used in the calculations and 1,180 males and 582 females if the period 1 May–15 July is used. Because dilution of proportions of marked turtles probably occurred constantly, these estimates may still be inflated. The similarity of the results of the 2 methods inspires some confidence in the probability that there were about 1,400 males on the main study area. The number of females is more difficult to judge due to inadequacy of samples but probably there were about 550 present. If these estimates of male and female numbers are accepted a sex ratio of 2.5 ♂♂:1 ♀ is obtained approaching the 1.98:1 ratio derived from capture data.

The magnitude of these estimates agrees 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 1 trap or hand collected in small areas mentioned previously demonstrate high population densities.

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Reproduction and Growth in the Turtle *Trionyx muticus*

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Major aspects of reproduction and growth in a population of *Trionyx muticus* from the Kansas River were determined from 448 recaptures of 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. Mature females are larger than mature males (mean plastron length ♀ = 154.2 mm; ♂ = 98.2 mm), have shorter tails, and they develop distinctive blotched carapacial patterns. Testes are largest in late fall and smallest in early summer. Females may lay two or more clutches per season. Clutch size (averaging about 11 eggs) and number of clutches per season are related to body size. Hatchlings have a mean plastron length of 24.5 mm and double in length by the end of their first year. Young males grow about 2 mm per month. Growth abruptly decreases at maturity. Females grow 2–3 mm per month until maturity. Growth rate then decreases but remains higher than in males. Growth in *T. muticus* is individually variable and changes from month to month and year to year.

BIOLOGY of trionychid turtles has not been studied in depth. Webb (1962) summarized the biology of North American species, mainly from short reports. Aspects of reproduction and growth in *Trionyx muticus* have been reported by Muller (1921), Cahn (1937), Goldsmith (1944), Anderson (1958), Webb (1962), Fitch and Plummer (1975) and Plummer (1977). I studied reproduction and growth in a population of *T. muticus* in the Kansas River near Lawrence, Douglas County, Kansas, approximately 39°N from July 1972 to May 1975. Fitch and Plummer (1975) reported preliminary observations from the years 1970–1972. Descriptions of the area and habitat have been recorded in other reports (Fitch and Plummer, 1975; Plummer and Shirer, 1975).

METHODS

Turtles were captured by hand or in wire mesh funnel traps, marked and released, or preserved for dissection. Approximately 3,700 captures were made of 2,700 turtles; 104 males and 102 females were dissected. The length of the plastron (PL) was measured midventrally with a plastic ruler to the nearest millimeter from the posterior edge to the anterior edge, including the marginal cartilaginous portion. The posterior edge of the carapace is subject to mutilation and its flexibility 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