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MOVEMENT PATTERNS IN A RIVER POPULATION OF THE SOFTSHELL TURTLE, *TRIONYX MUTICUS*

By

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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*.

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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.

We 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 8½ ft. (¼ 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 RMIRT2 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

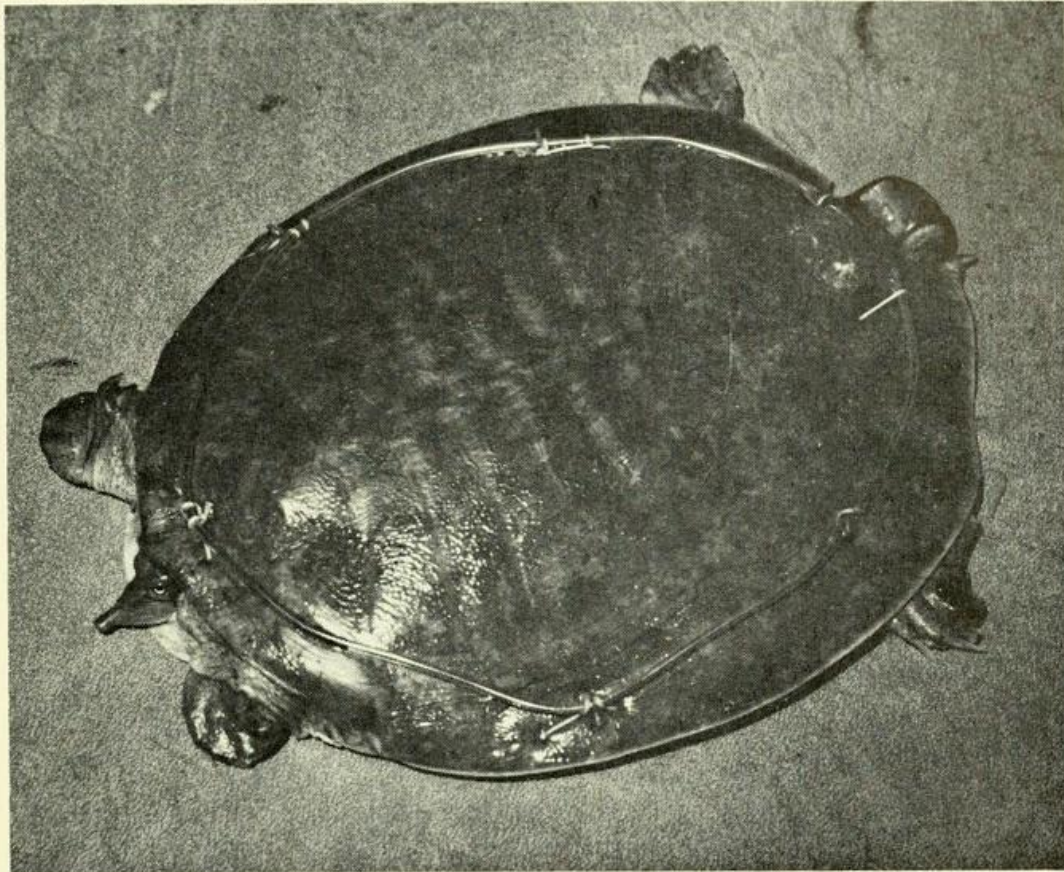


FIG. 1.—Female *T. muticus* with transmitter sewn onto the edge of her carapace at six different points.

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 (12x140 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 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



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

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, to date, approximately 3500 captures on 2500 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 mid-ventrally from the most anterior cartilaginous portion to the posterior edge.

ACKNOWLEDGMENTS

We sincerely thank the Don Cain and Dean Cain families for permitting us to use their property to gain access to our study area, for furnishing space for storage of our boat, for providing turtles caught on their fishing lines, and for their constant, genuine concern for the progress of our work. Henry S. Fitch originally suggested the study and critically reviewed the manuscript. Richard Patton was an industrious field assistant in 1974. Steve Everly, former photographic technician of the Center for Research, Inc., University of Kansas, provided the aerial photographs. Melvin L. Thompson, U.S. Geological Survey, provided daily water level readings. Richard Lattis instructed Plummer in the assembling of transmitters.

Jan Wagner supplied the Pigmy Current Meter. Alan H. Savitzky and Sharon E. Plummer read portions of the manuscript. An anonymous reviewer provided many helpful suggestions. We thank Sharon Plummer for typing the manuscript. This study was supported by a grant from the General Research Fund, University of Kansas, and by a Graduate School Summer Fellowship to Plummer.

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, in press), and nesting occurs from early June to mid-July (Fitch and Plummer, in press). 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 0.6 of the depth as one descends into the column. Velocities were taken in depths ranging from 0.6–1.2 m.

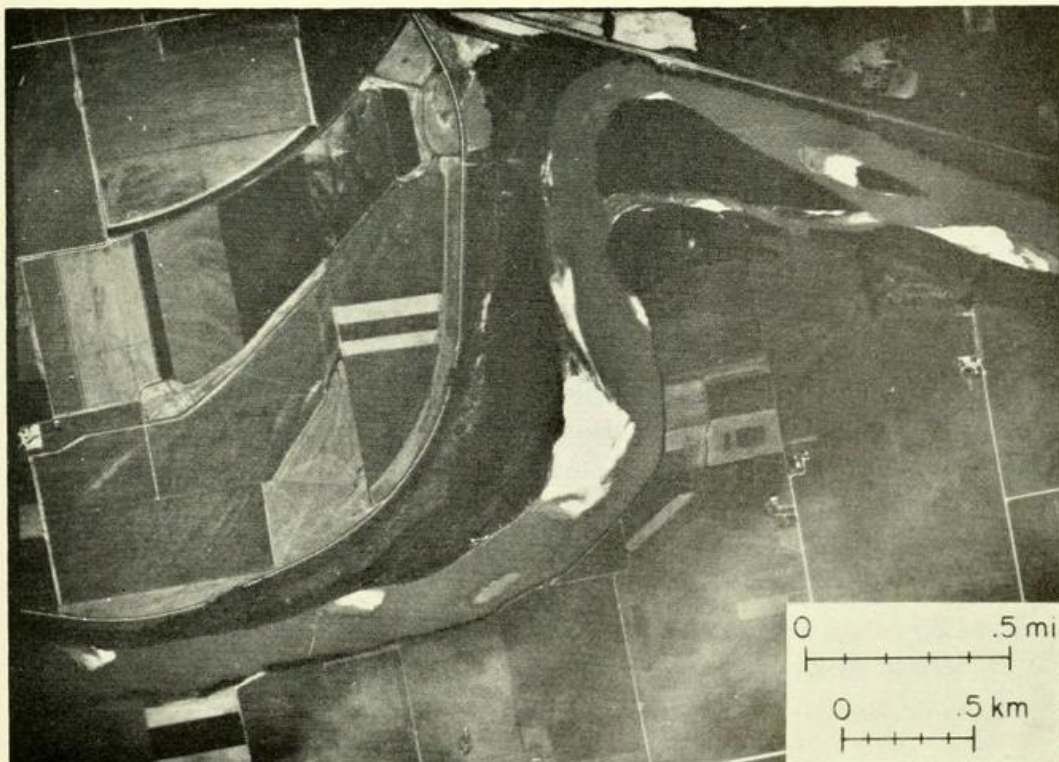


FIG. 3.—Aerial photograph of the main study area taken 5 September 1974.



FIG. 4.—Habitat of *T. muticus*, sandbar at main study area.

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, in prep.). 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 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 sand-

bars 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., Koeppel, 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, In Press), 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.

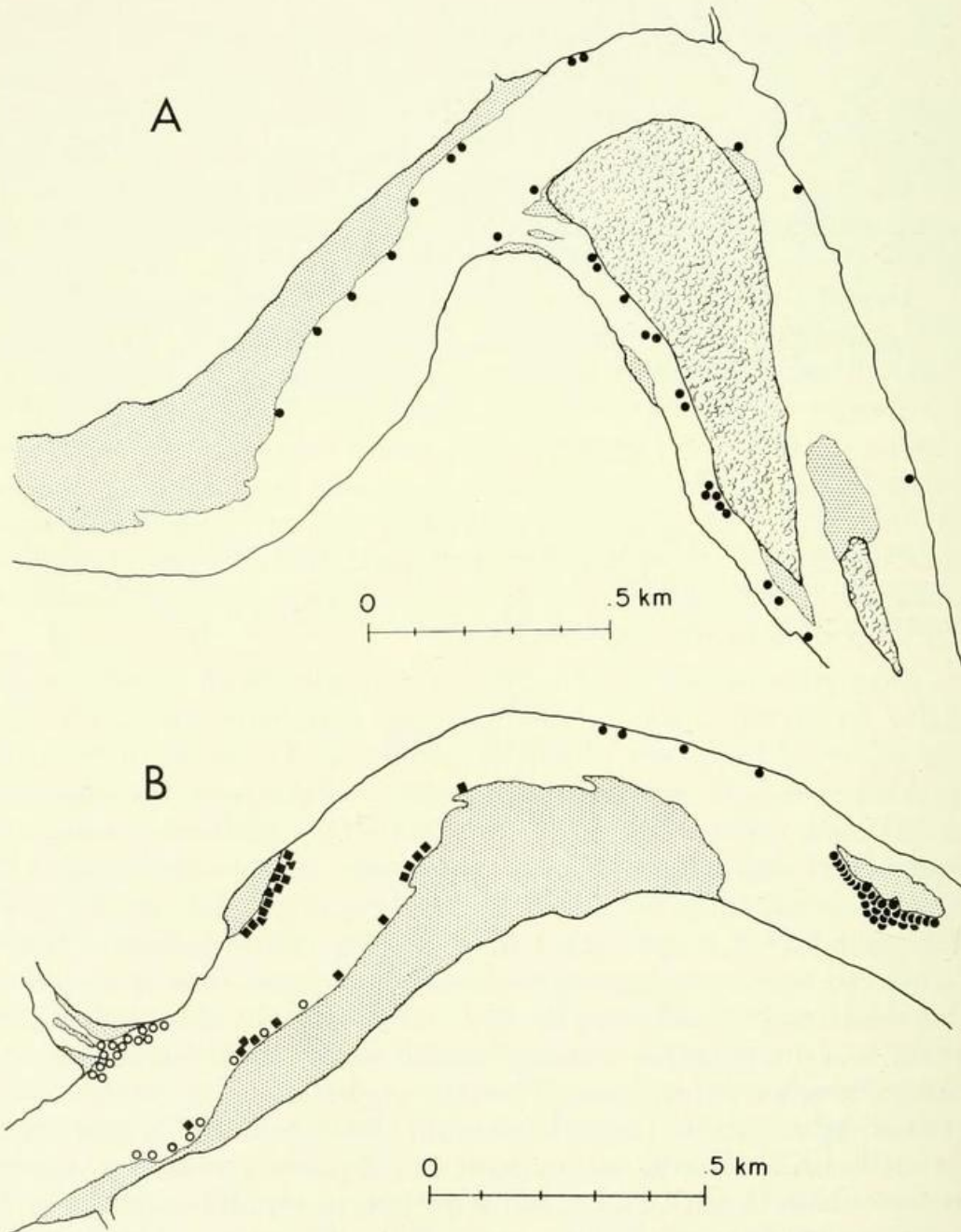


FIG. 5.—Locational points in home ranges of *T. muticus*. A. Adult female home range. The entire area is covered in several days; the turtle crossed the river frequently. B. Home ranges of three males. Note closely clustered points. These males crossed the river infrequently. Stippled areas indicate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

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.

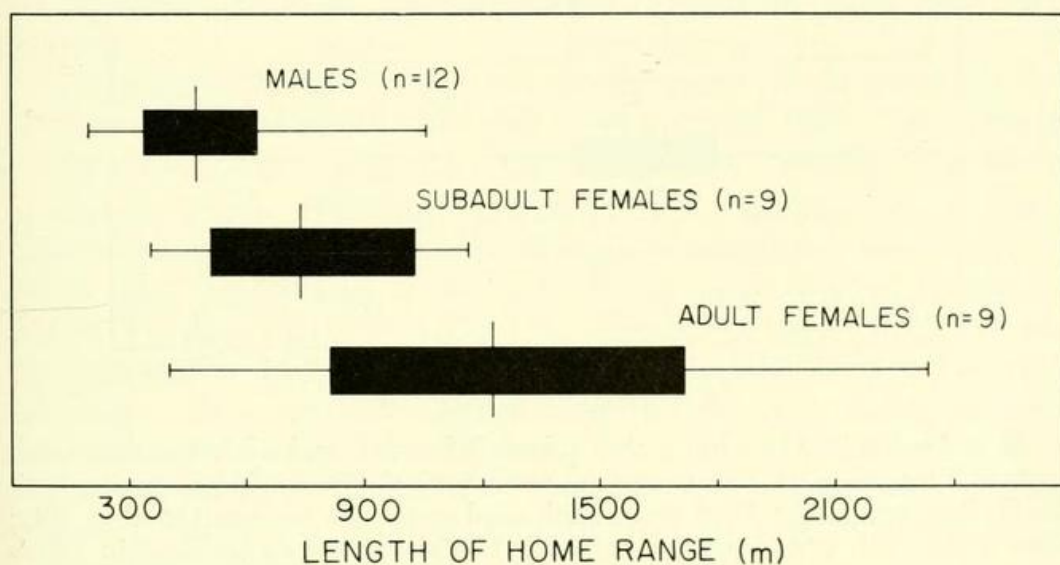


FIG. 6.—Sizes of home ranges in adult males, subadult females, and adult females. Long vertical lines are means; rectangles are asymmetrical 95% confidence limits; horizontal lines are ranges. All means are significantly different from one another ($\delta \delta$ vs. adult $\text{♀} \text{♀}$, $P <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

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 (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 summa-

rizes 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.

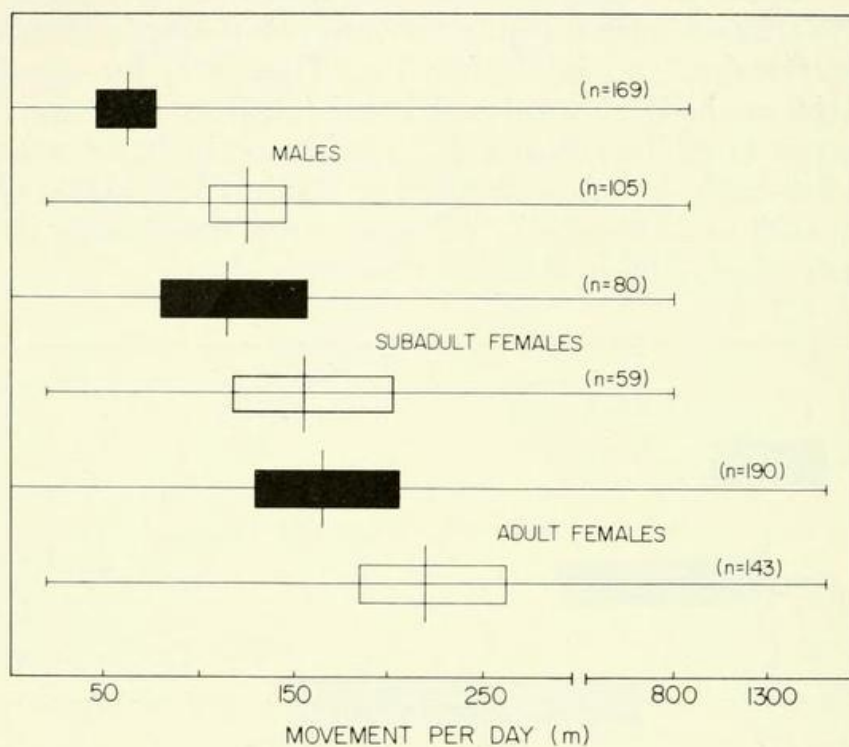


FIG. 7.—Vagility in adult males, subadult females, and adult females. Long vertical lines are means; rectangles are asymmetrical 95% confidence limits; horizontal lines are ranges. Dice grams with solid rectangles represent total vagility; dice grams with open rectangles represent total vagility minus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

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 dis-

tances in their home ranges than do males, it is not surprising to find that 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 through 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 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

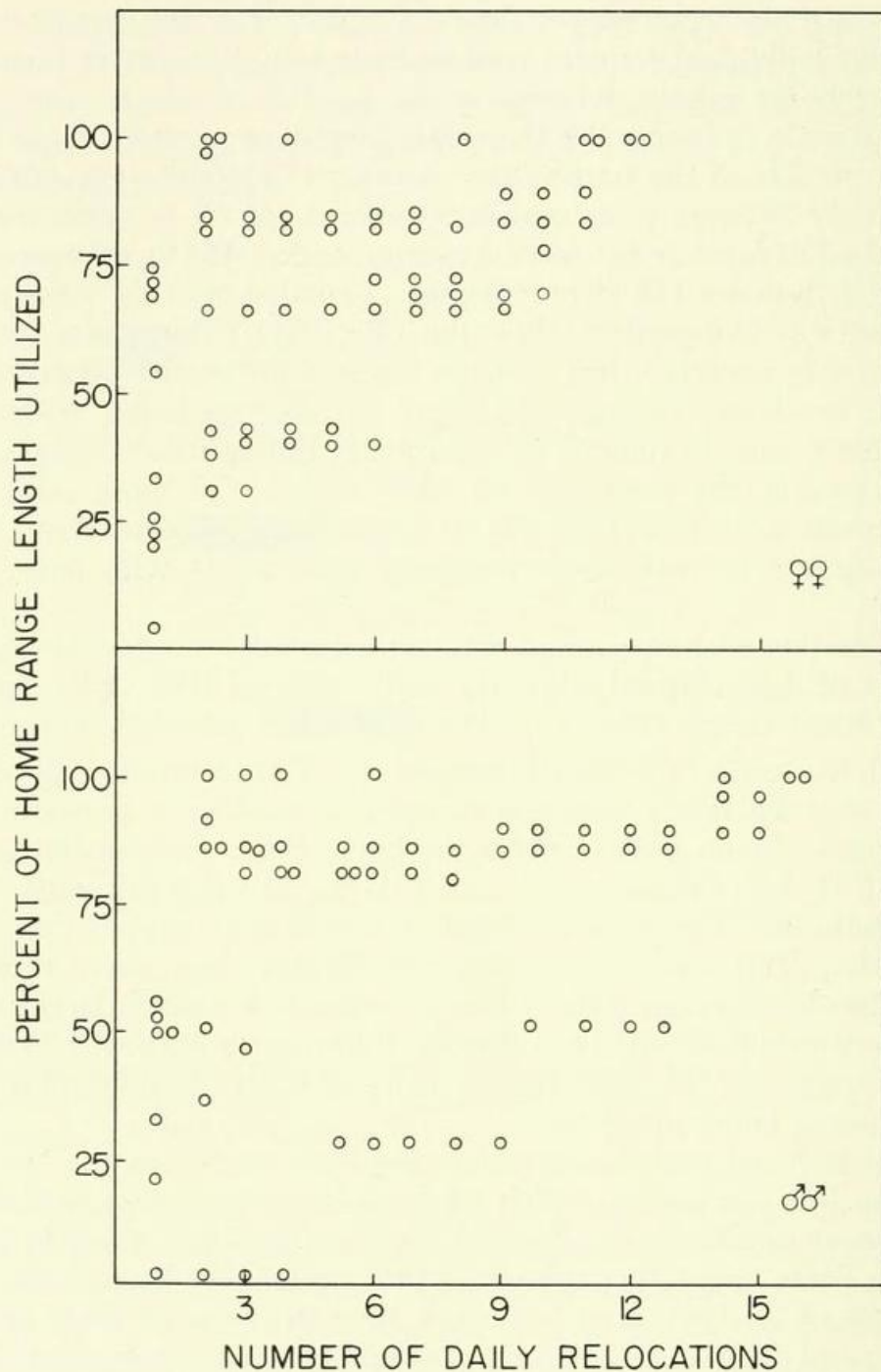


FIG. 8.—The relationship between percent of home range utilized and time (number of days), in males and females. Females moved over area of home range somewhat faster than males; on the average however, difference is not significant.

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 described below males moved up- and downstream, establishing home ranges of varying duration. Shifting of

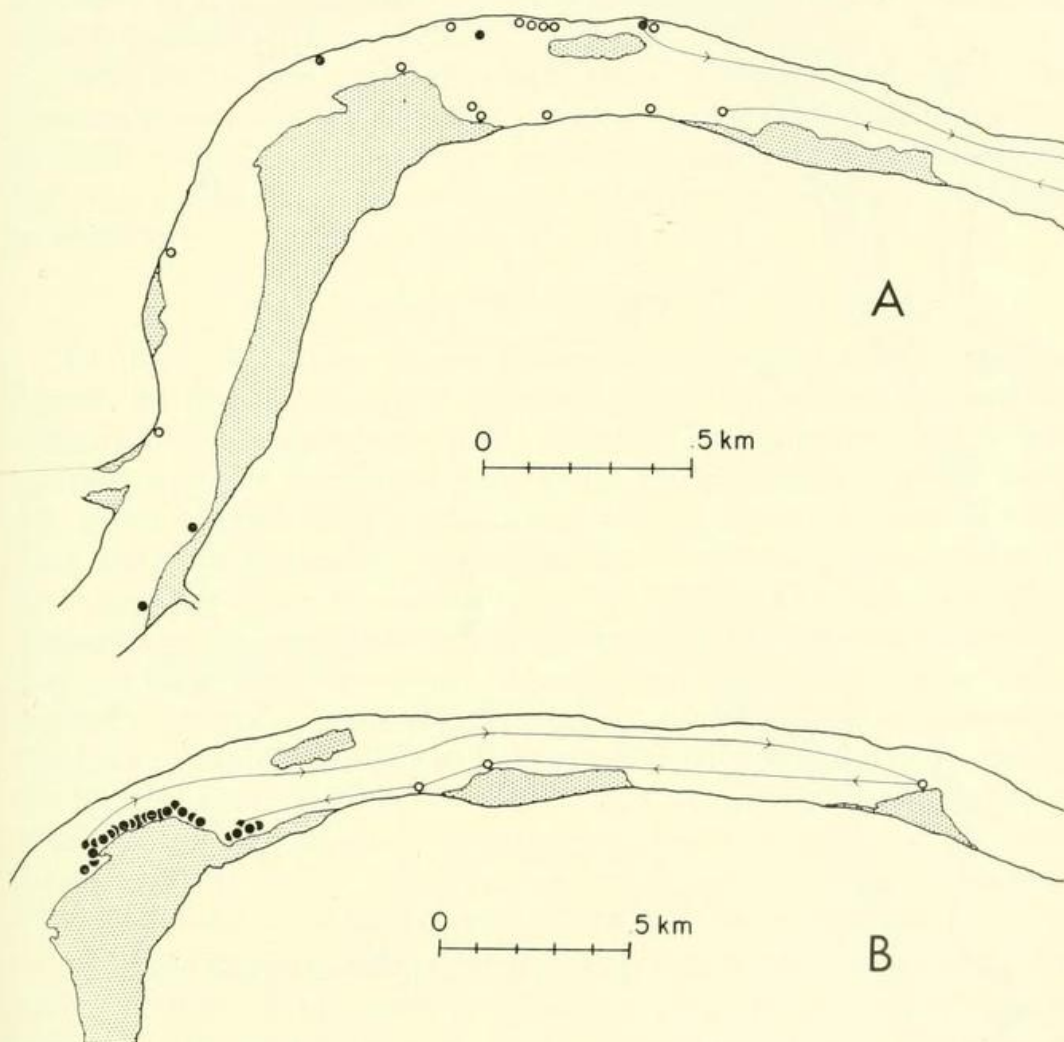


FIG. 9.—Temporary movements (“sallies”) out of the home range. A. Female which made a 4000 m upstream sally of 7 days; downstream return movement was made in one day. Closed circles are locations recorded before the sally; open circles are locations recorded after the sally. This unusually long movement 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.

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.

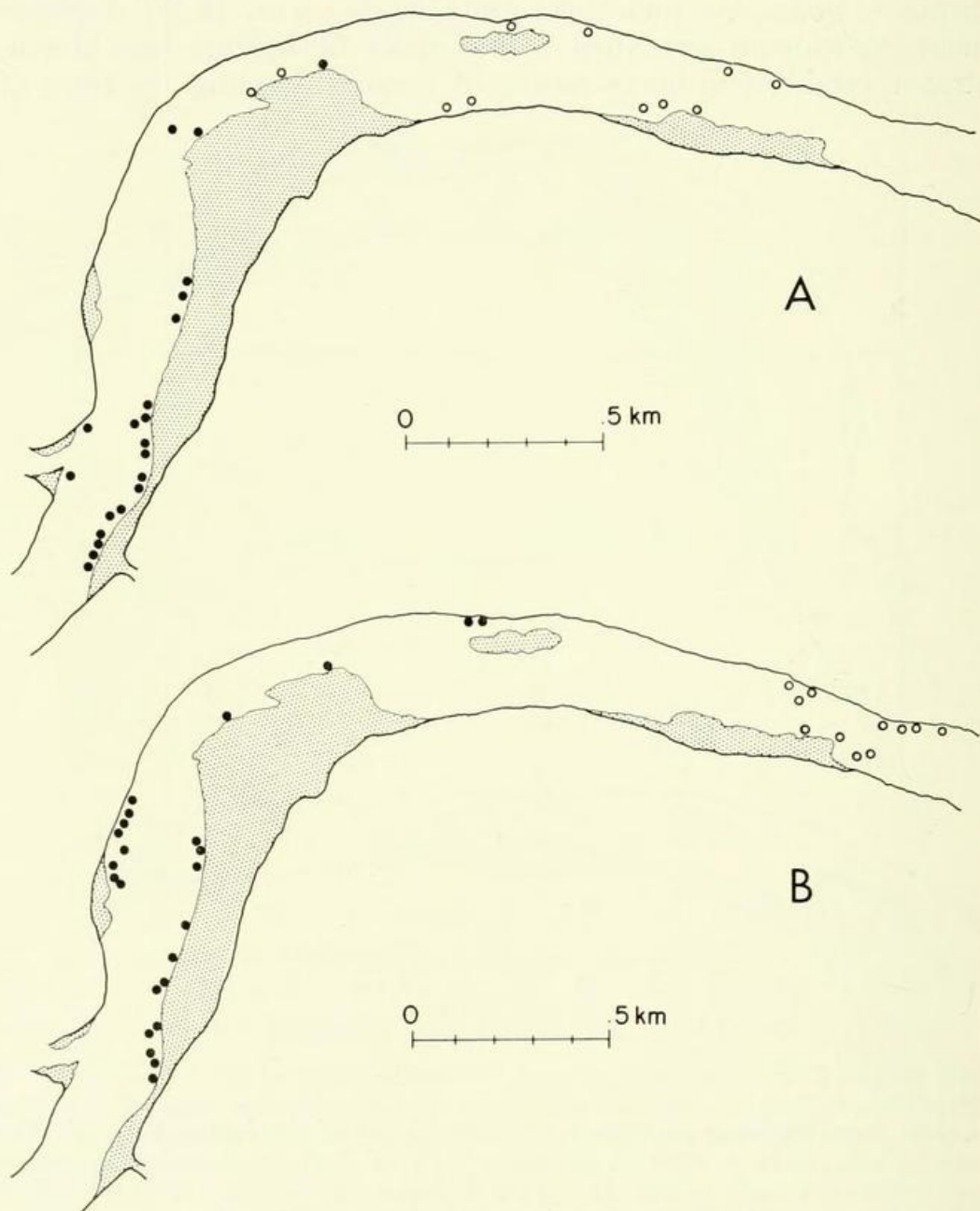


FIG. 10.—Shifts in home range location in a subadult female and an adult female, respectively. A. Closed circles are locations recorded from 6 Jun. to 28 Jun.; open circles are locations recorded from 29 Jun. to 7 Jul. The shift represents a mean upstream movement of 1363 m. B. Closed circles are locations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

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, we 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 summa-

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. SUB-ADULTS 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	-----

izes early season movement patterns of four females, two of which eventually settled into home ranges, comparable to those maintained after the nesting season.

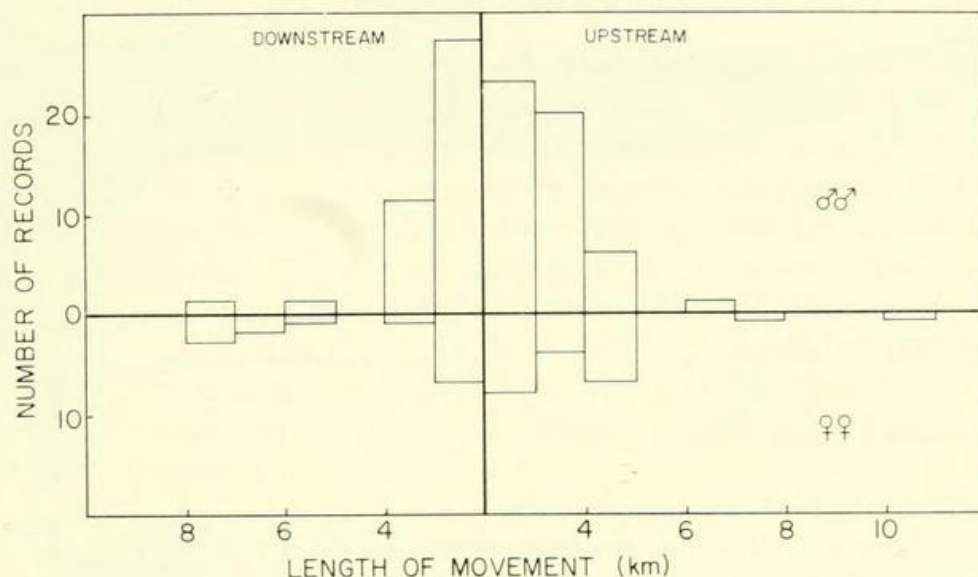


FIG. 11.—Histogram of long movements in males and females. Both sexes appear to make long movements up- and downstream.

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 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 sud-

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

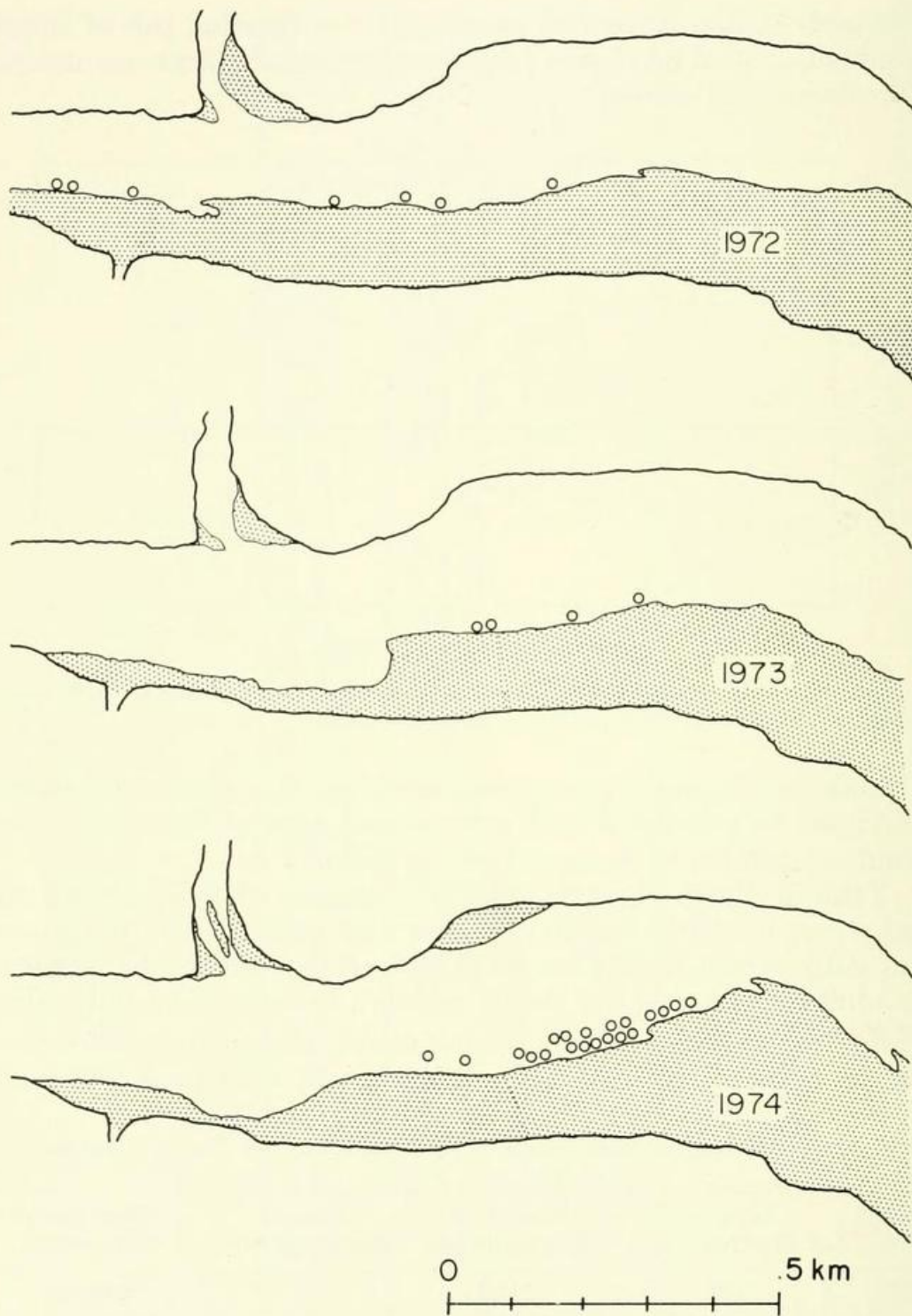


FIG. 12.—Locations recorded for the same subadult female *T. muticus* in three consecutive years; by balloon tagging in 1972; recaptures in 1973, and radiotelemetry in 1974.

den variations in strength, and were in the main channel removed from the shoreline. These characteristics suggest that when making long movements during a home range sojourn, turtles travel in deeper, more open water than they frequent ordinarily. 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.

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 nesting season. Two adults displaced 2700 m upstream, were

TABLE 3.—FATE OF DISPLACED TURTLES EQUIPPED WITH TRANSMITTERS.

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

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

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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 establish-

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 next year
569	92	3	Returned to area of initial capture

ing 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 our 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 upstream 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. We have found that this species is highly vagile, with a distinct, significant difference in vagility between males and females.

Our 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 our 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 our 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 our 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 our 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 relocated 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 our 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, in prep.). 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* from July 1972 to October 1974. Three methods were utilized: 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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