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Activity, Habitat, and Movement Patterns of Softshell Turtles (*Trionyx spiniferus*) in a Small Stream

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ABSTRACT. – **Adult individuals of *Trionyx spiniferus* were monitored with radiotelemetry daily over two years in Gin Creek, a small, narrow (ca. 5 m wide) urban stream in central Arkansas. Softshells were active on ca. 45% of 1500 observations. All movements not related to nesting or basking were aquatic. Records of over 1800 daily movements by 16 individuals demonstrated that softshells were limited spatially to a central ca. 2.5 km of the ca. 6 km long stream. Both upstream and downstream boundaries to movement were clearly defined and each occurred at a point of distinct habitat change. Softshells spent most of their time in pool habitats with most movements being either within or between pools. Males spent more time in riffle habitats (9%) than did females (< 1%). Males and females moved on about 85% of days, averaging about 141 m/d and 122 m/d, respectively. Coefficients of variation were low for frequency of movement (males, 3%; females, 11%), but well above 100% for amount of movement per day for most individuals. Daily movements were along the longitudinal axis of the creek. The annual home range length averaged 1750 m for males and 1400 m for females; corresponding values for home range areas were 0.88 and 0.70 ha. The annual home ranges of some softshells appeared graphically as either a discrete narrow or wide utilization distribution and were adequately described by the annual home range value. For other turtles, describing the home range with a single annual value obscured considerable within-year temporal variability resulting from either using different portions of the annual home range at different times of the year and/or making brief long-range excursions out of the home range. The home ranges of individual turtles were similar between years. Over the course of the study, 30 long movements (> 900 m/d) were made throughout the year by 10 different softshells, including both sexes, most of which resulted in a return to the starting location within a few days.**

KEY WORDS. – **Reptilia; Testudines; Trionychidae; *Trionyx spiniferus*; turtle; ecology; radiotelemetry; home range; movements; activity; habitat; Arkansas; USA**

The dynamic use of space by mobile animals has important demographic, genetic, and evolutionary consequences (Brown and Orians, 1970). The use of space by reptiles reflects in part the use of resources in a particular environment and thus would be expected to vary in different environments (Gibbons and Semlitsch, 1987; Schubauer et al., 1990). Most useful for comparisons of the use of space in different aquatic environments should be studies using similar techniques conducted in habitats differing in relatively few parameters (e.g., small vs. large streams). Movements of aquatic turtles have been studied by mark-recapture (e.g., Cagle, 1944; Ernst, 1970; Bury, 1979) and/or radiotelemetry (e.g., Moll and Legler, 1971; Plummer and Shirer, 1975; Schubauer et al., 1990; Jones, 1996). Telemetry may yield substantially different quantitative results from those of mark-recapture even on the same individual turtles (Schubauer et al., 1990; Yabe, 1992). In general, telemetry should be superior for short-term intrapopulational movement studies because the amount of data that can be collected in a relatively short time is large and because the investigator can control sampling effort and monitor where individual turtles actually go instead of being limited to sporadic sampling where collecting is productive. In addition, telemetry is useful for identifying short-term behaviors such as irregular wanderings (Brown and Orians, 1970; Plummer and Shirer, 1975).

Movement patterns of turtles in small streams, of trionychid turtles in general, and of *Trionyx spiniferus* in particular, are poorly known. Terrestrial movements of *T. spiniferus* that are not associated with basking or nesting are extremely rare and apparently may be stimulated by falling water levels in ponds (summarized in Webb, 1962; Williams and Christiansen, 1981). The only existing aquatic movement data on *T. spiniferus* are those of Breckenridge (1955), who concluded that, based on 30 recaptures of 172 marked individuals, there was little aquatic movement resulting in spatial displacement of individuals, and those of Graham and Graham (1997), who showed that telemetered softshells moved about 3 km upriver from a lake in the fall and returned to the lake in the spring. In this paper, we describe the spatial use of habitat and patterns of daily movement determined by telemetry in a population of the spiny softshell turtle, *T. spiniferus*, inhabiting a small urban stream. We compare our results to other telemetry studies on stream-dwelling turtles, especially to those on a large river population of *T. muticus* (Plummer and

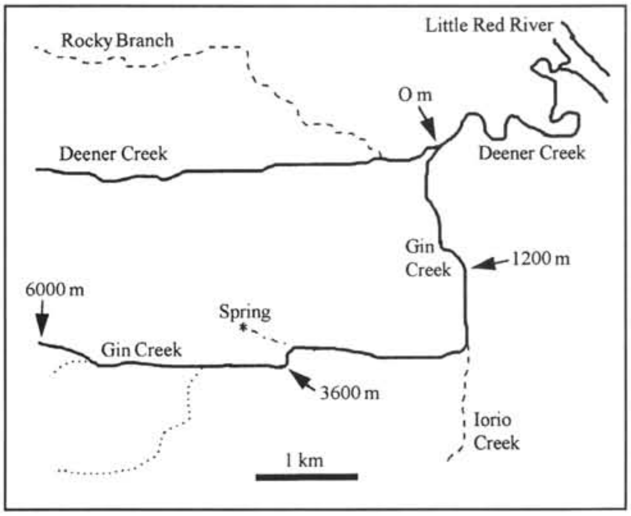

Figure 1. Map of Gin Creek, Arkansas, and associated drainage systems. Dashed lines indicate small streams which often dried or stagnated in the summer. Dashed-and-dotted line indicates the spring run. Dotted lines indicate major drainage ditches. Arrows indicate locations in meters upstream from the mouth of Gin Creek. On Gin Creek, *Trionyx spiniferus* occupied the stretch approximately between locations 1200 and 3600 m.

Shirer, 1975; Plummer, 1977), the sister species of *T. spiniferus* (Meylan, 1987).

The generic allocation of softshells has been disputed and unsettled since Meylan (1987) subdivided the genus *Trionyx*. Until settled, rather than adopting the name *Apalone* recommended by Meylan (1987) for American softshells, we follow Webb (1990) and Ernst et al. (1994) in retaining the generic name *Trionyx*.

MATERIALS AND METHODS

Gin Creek is a small, ca. 6 km long, partially spring-fed first-order stream in the Little Red River drainage system in Searcy, White County, Arkansas. Gin Creek empties into the lower reaches of Deener Creek which then empties into the Little Red River ca. 3 km downstream (Fig. 1). Because the spring run enters Gin Creek ca. 3.5 km upstream from the creek mouth, most of the upper 2.5 km of the creek is often stagnant or mostly dry during the summer whereas the lower 3.5 km flows more or less throughout the year. Most of Gin Creek passes through urban areas and thus receives a large amount of runoff from storm sewers, pavement, and other nonporous surfaces. Water levels can rapidly rise 1–2 m during heavy rains but will also rapidly fall afterwards. Substrate in the upper 4.8 km of the creek is mostly hard clay, whereas most of the lower 1.2 km is shale bedrock. Frequent scouring of the creekbed results in unconsolidated sediments being limited to deeper pools, shallow slower waters of inside bends, and small backwater areas created by snags.

Our preliminary observations suggested that *T. spiniferus* in this small population (< 60 adults, MVP, unpubl. data) was limited to a central ca. 2.5 km of Gin Creek, probably because substrate in the lower ca. 1.2 km was bedrock, and thus did not provide suitable burying sites, and the upper ca. 2.5 km usually stagnated or dried in the summer. Within the central ca. 2.5 km, the creek ranges from ca. 2 to 7 m in width (average ca. 5 m) and has alternating shallow riffles and deeper pools with a substrate of highly dissected hard clay. At normal summer water levels, depth averages ca. 35 cm and is highly variable over short distances, ranging from < 10 cm in riffles to ca. 100 cm in the deeper pools (Fig. 2). A beaver (*Castor canadensis*) dam created the largest pool (ca. 100 m long) in the creek. In this pool, and at several other smaller natural pools, underwater burrows dug into the bank by both beaver and muskrat (*Ondontra zibethicus*) created possible refugia for *T. spiniferus*. In addition to softshells, other turtles in Gin Creek include common snappers (*Chelydra serpentina*), common musk turtles (*Sternotherus odoratus*), eastern mud turtles (*Kinosternon subrubrum*), cooters (*Pseudemys concinna*), and sliders (*Trachemys scripta*).

We captured *T. spiniferus* either by hand or with chicken wire turtle traps (Plummer, 1977). For each softshell, we determined sex, measured plastron length (PL) and body weight, gave it a unique mark (Plummer, 1977), attached a transmitter (Model SM-1, AVM Instrument Co., Ltd., Livermore, CA, or Model raw pot one-stage, L.L. Electronics, Mahomet, IL, or Model CHP-2P, Telonics, Inc., Mesa, AZ) to the posterior portion of the carapace with stainless steel wire, and released it at the site of capture. All transmitters had masses < 0.4% of turtle mass.

With few exceptions, we located each softshell daily during the activity seasons (March to mid-November) of 1994 and 1995. For each observation, we recorded the turtle's behavior, habitat, and location by comparison to known positions along the creek which were marked with plastic flagging (designating locations as 0 to 6000 [meters] from the mouth of Gin Creek, with most observations made at locations from ca. 1200 to 3600). We also recorded the occurrence of precipitation and qualitative conditions of water clarity and depth.

Linear home range, i.e., the statistical range of locations along the stream, was calculated. Home range area was also calculated by multiplying linear home range times the aver-

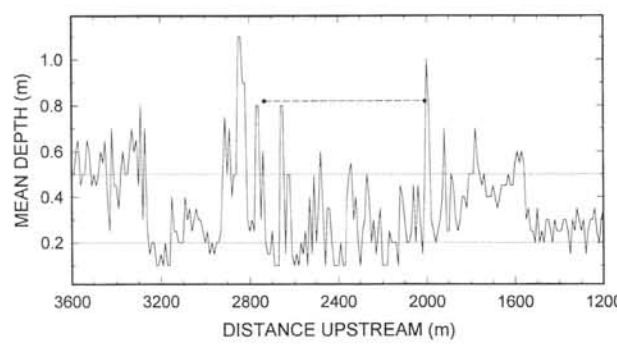

Figure 2. Mean depth of Gin Creek plotted each 10 m in the stretch favorable for *Trionyx spiniferus*. Locations represent upstream distances from the creek mouth. Major pool areas extend roughly from locations 3250–3600 m, 2750–2950 m, and 1550–2000 m. The major riffle area extends from locations 2000–2750 m and is indicated by the dashed line. Dotted lines provide 0.2 and 0.5 m depth references.

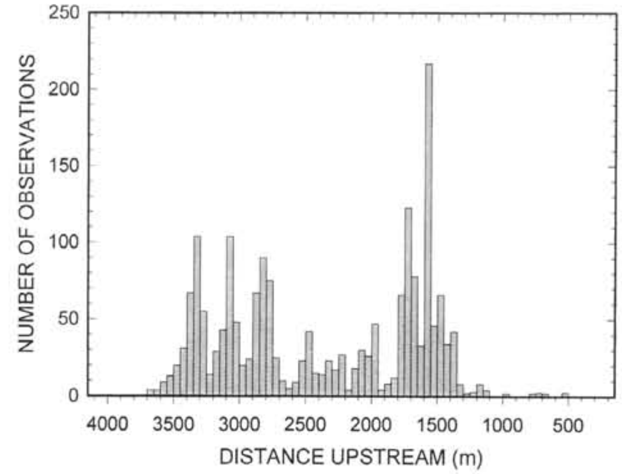

Figure 3. Daily observations (n = 1855) according to location of 16 telemetered *Trionyx spiniferus* in Gin Creek in the activity seasons of 1994 and 1995.

age width of stream. Statistical analyses were conducted with SYSTAT (SYSTAT, 1992). Unless otherwise stated, means are accompanied by ± one standard deviation.

RESULTS

Activity. — *Trionyx spiniferus* in Gin Creek were diurnal. The only nocturnal activity that we observed was apparently caused when we attempted to capture telemetered softshells immediately after dusk. Softshells were active (i.e., moving) on 665 of 1507 (44.1%) observations. Because we determined activity directly by visual confirmation as well as indirectly by the waxing and waning of signal strength, all activity estimates are minimum values. Activity in males and females was equally frequent (males, 46.8%, n = 620; females, 42.3%, n = 887; χ^2 = 2.99, $p > 0.05$). For inactive turtles with known behaviors, males tended to bury in sediment more frequently than females (males, 82.9%, n = 252; females, 65.6%, n = 90; χ^2 = 11.82, $p < 0.001$). However, this difference may reflect the relative ease with which we found males, which tended to bury at the water's edge, compared to females, which tended to bury in deeper water.

Macrohabitat. — All movements by *T. spiniferus* in Gin Creek were aquatic. The only softshells observed out of water were basking, usually within 30 cm of water, or nesting (n = 4), all within 2–3 m of water. Although Gin Creek was ca. 6 km in length, 1855 observations of 16 telemetered turtles clearly demonstrated that softshells primarily restricted their activities to a stretch of creek ranging approximately from locations 1350 to 3450 (Fig. 3). Of 7 softshells that made one-day long distance (i.e., > 900 m) movements downstream past location 1650, each stopped its movement between locations 1155 and 1646. Only 23 (1.2%) of 1855 total observations were downstream from location 1300 (Fig. 3). Fourteen (61%) of these occurred concurrently in 1994 by 3 turtles on days of heavy rain and high water. Each turtle subsequently returned upstream. Only 8 observations downstream from location 1300 occurred during periods when normal water levels prevailed and these were all made by one turtle. The maximum distance moved below location 1300 was 775 m. The downstream boundary to softshell movements occurred roughly at a point of distinct habitat change which then continued downstream another 1200 m to the creek mouth. There were few pools in this area and the substrate was loose rock or bedrock with little or no sand or silt.

Table 1. Frequency of movement (no. of days in which there was movement recorded ÷ total no. days observed), amount of daily movement (including [i] and excluding [e] days in which there was no recorded movement), coefficient of variation (CV) for amount of daily movement, and annual home range length (m) and area (ha) for 7 adult male and 9 adult female *Trionyx spiniferus* in Gin Creek, Arkansas. A minimum of 30 consecutive days of tracking was required for inclusion.

Turtle no.	Year	Frequency of Movement	Daily Movement [m/d (n), i or e]	CV (%)	Annual Home Range [m or ha]
Males					
3	94	0.83	233 ± 266 (69) i	114	2310 m
			282 ± 268 (57) e	95	1.16 ha
17	95	0.90	86 ± 136 (111) i	158	1667 m
			95 ± 140 (100) e	147	0.83 ha
46	94	0.90	119 ± 113 (99) i	95	784 m
			132 ± 111 (89) e	84	0.39 ha
46	95	0.86	73 ± 120 (187) i	164	2093 m
			85 ± 125 (161) e	147	1.05 ha
48	94	0.86	156 ± 183 (63) i	117	1450 m
			182 ± 185 (54) e	102	0.73 ha
48	95	0.87	128 ± 265 (164) i	207	2160 m
			148 ± 279 (142) e	189	1.08 ha
49	95	0.93	192 ± 280 (147) i	146	1829 m
			206 ± 286 (137) e	139	0.91 ha
Male Means					
		0.88 ± 0.03	141 ± 57 (7) i	143	1756 ± 522 m
			161 ± 69 (7) e	129	0.88 ± 0.26 ha
Females					
4	95	0.75	53 ± 74 (207) i	140	683 m
			70 ± 78 (155) e	111	0.34 ha
5	94	0.95	239 ± 342 (44) i	143	2140 m
			251 ± 346 (42) e	138	1.07 ha
7	94	0.65	70 ± 150 (40) i	214	1030 m
			107 ± 176 (26) e	164	0.52 ha
16	95	0.79	76 ± 166 (229) i	218	1688 m
			96 ± 181 (181) e	189	0.84 ha
44	94	0.88	288 ± 374 (58) i	130	2145 m
			327 ± 382 (51) e	117	1.07 ha
45	94	0.89	131 ± 157 (35) i	120	855 m
			148 ± 159 (31) e	107	0.43 ha
45	95	0.90	115 ± 260 (62) i	226	1040 m
			127 ± 271 (56) e	213	0.52 ha
63	95	0.91	56 ± 94 (137) i	168	1125 m
			62 ± 97 (124) e	156	0.56 ha
80	95	0.84	72 ± 250 (121) i	347	2072 m
			85 ± 271 (102) e	319	1.04 ha
Female Means					
		0.84 ± 0.09	122 ± 85 (9) i	190	1420 ± 590 m
			141 ± 90 (9) e	168	0.71 ± 0.29 ha

The upstream boundary of softshell distribution likewise was clearly defined. Only 33 (1.8%) of 1855 total observations were upstream from location 3480 (Fig. 3). Twenty-two (66.7%) of these were made by one turtle and the remaining 11 were distributed among 3 other turtles. The maximum distance moved above location 3480 by any turtle was 220 m. Of 5 softshells that made one-day-long movements (> 900 m) upstream past location 3250, all 5 stopped their movements between locations 3280 and 3320. The upstream boundary to softshell movements occurred ca. 200 m above the entrance of the spring run into Gin Creek (location 3480), and in part was a backwater from the spring run. Above this backwater, the creek was very shallow with few pools and subject to stagnation and drying in the summer.

Microhabitat. — Within the favorable ca. 2.5 km stretch of creek, observations of *T. spiniferus* were concentrated in two major areas, located at roughly 2750–3400 and 1350–1800 (Fig. 3). Both areas had a high ratio of pools to riffles.

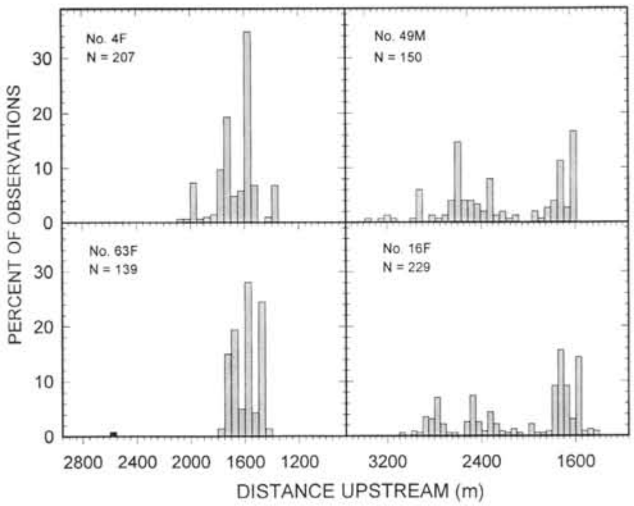

Figure 4. Typical home ranges of four *Trionyx spiniferus* in Gin Creek. No. 4 (female): bars indicate area occupied 1 March – 27 September 1995; No. 49 (male): bars indicate area occupied 22 May – 27 October 1995; No. 63 (female): shaded bars indicate area occupied 1 June – 25 October 1995, solid bar indicates location after a 900 m excursion from location 1675 on 23 August, turtle returned to location 1580 on 24 August; No. 16 (female): bars indicate area occupied 16 October 1994 – 25 October 1995.

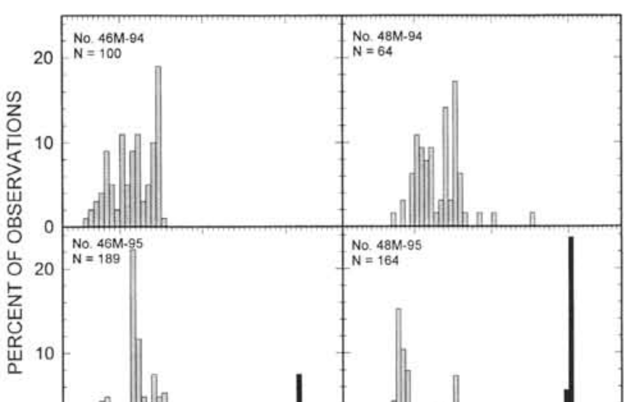

Figure 5. Comparisons of annual home ranges of two *Trionyx spiniferus* in two separate years. No. 46 (1994): bars indicate area occupied 9 June –18 September; No. 46 (1995): shaded bars indicate area occupied 17 April – 1 May and 27 May – 18 October, solid bars indicate area occupied 2–25 May and again 19–27 October; No. 48 (1994): bars indicate area occupied 20 June – 23 August; No. 48 (1995): shaded bars indicate area occupied 2 May – 1 September, solid bars indicate area occupied 2 September – 19 October, open bar indicates location after a 1900 m excursion from location 3250 on 14 July, turtle returned to location 3300 on 15 July.

Pools in the upstream area were either natural large pools or water backed up behind a small man-made dam. Pools in the downstream area resulted primarily from water backed up behind a beaver dam. The low observation frequency between locations 1800–2750 (Fig. 3) occurred in a stretch of creek with a low ratio of pools to riffles (Fig. 2) resulting from large riffles and small pools (many < 1–2 m in diameter).

Inactive softshells buried into loose bottom sediments, and occasionally took refuge in muskrat or beaver burrows. Active softshells were usually in pools and most movements were either within or between pools. Although untelemetered hatchlings and juveniles were commonly observed in riffles, telemetered adult softshells generally avoided this microhabitat. Adult males were observed in riffles more often (70 of 803 [8.7%] observations) than adult females (6 of 813 [0.7%] observations; $\chi^2 = 57.4, p < 0.001$). Because the pool areas of most intensive use by softshells were on opposite ends of the central riffle area and individual turtles often used both pool areas, they had to move through the large riffle – small pool area in between. We observed that turtles moving through this area moved quickly from pool to pool, many of which were < 1–2 m in diameter. In this area, softshells were observed in riffles 2–3 times more often than the creek in general (males, 27 of 155 [17.4%] observations; females, 3 of 139 [2.2%] observations).

Frequency and Amount of Movement. — *Trionyx spiniferus* moved on approximately 85% of days (Table 1). This value is a minimum frequency because we could not detect movements between successive days if individual softshells returned to the same site as on the previous day. Although the movement frequency for males (0.88) was slightly greater than that for females (0.84), the difference was not significant ($t = 1.14, p > 0.25$, df = 14). Males tended to move further than females each day whether or not days of no movement were included (Table 1), but the differences were not significant (included, $t = 0.53, p > 0.50$, df = 14; excluded, $t = 0.51, p > 0.60$, df = 14). Coefficients of variation for frequency of movement among individuals were 3.4% for males and 10.7% for females, whereas variability in amount of daily movement by individuals was large, with coefficients of variation well over 100% for most individuals (Table 1).

Home Range. — Gin Creek is narrow, and all movements that we detected were along the longitudinal axis of the creek. Thus, home ranges were described as linear utilization distributions, such as used by other turtle researchers working in stream habitats (e.g., Moll and Legler, 1971; Sharber, 1973; Florence, 1975; Plummer and Shirer, 1975; Yabe, 1992; Jones, 1996). Home ranges of some *T. spiniferus* were graphically identified by either a narrow (e.g., Fig. 4, turtles no. 4 and 63) or wide (e.g., Fig. 4, turtles no. 49 and 16) cluster of points. Such discrete home ranges were adequately described by the annual home range size (i.e., the statistical range of locations from an entire activity season). Annual home range size was slightly larger in males than females, but not significantly so (Table 1; $t = 1.21, p >$

Table 2. Comparison of home range length and area of aquatic turtles from telemetry studies conducted in lotic (riverine) habitats. Home range area for *T. muticus* was calculated assuming an average width of 175 m for the Kansas River and that adult females used the entire width whereas adult males used 50% of the width (Plummer and Shirer, 1975). Home range length and area for *T. spiniferus* were averaged for the two sexes.

Species	Average Width of Stream (m)	Home Range Length (m)	Home Range Area (ha)	Citation
Chelydra serpentina	13	426	0.6	Sharber, 1973
Trachemys scripta	90	287	3.6	Moll and Legler, 1971
	24	274	0.7	Florence, 1975
Pseudemys concinna	175	340	1.4	Buhlmann and Vaughan, 1991
Graptemys flavimaculata	100	1644	3.8	Jones, 1996
Mauremys japonica	3	74	0.02	Yabe, 1992
Trionyx muticus	175	797	11.6	Plummer and Shirer, 1975
Trionyx spiniferus	5	1567	0.8	This study

0.20, df = 14). Assuming an average width of 5 m for Gin Creek, calculated home range areas were 0.88 ha for males and 0.70 ha for females (Table 1).

For some softshells, a single value of annual home range size obscured considerable within-year temporal variability. For example, some turtles used different portions of their annual home range at different times of the activity season (e.g., Fig. 5, turtles no. 46-95 and 48-95 and Fig. 6, turtle no. 17), and other turtles made brief long-range excursions out of an otherwise discrete home range (e.g., Fig. 4, turtle no. 63 and Fig. 5, turtle no. 48-95).

Three individual softshells were tracked for a sufficient number of days in each of two years to permit between-year comparisons. At least portions of the 1994 and 1995 annual home ranges for female no. 45, and males no. 46 and 48 were similar in size and location (Table 1; Fig. 5).

Long Movements. — Thirty long movements (i.e., > 900 m/d) occurred throughout the activity season (April, n = 1; May, n = 1; June, n = 6; July, n = 10; August, n = 3; September, n = 7; October, n = 2). Thirteen of these movements were made by 5 different males and 17 movements by 5 different females. Of the 16 long movements made in June – July, 11 were by females. Of the overall 30 movements 16 were downstream and 14 were upstream. Direction of movement was unrelated to whether water levels were normal or high (Fisher Exact Test, p = 1.00). Twenty movements were followed in 2–3 days by a return to the original location. At least 4 other movements were followed by a slower return over 6–14 days. Two cases of long excursions, interesting because of their concurrence in space and time, began on 13 July 1995 when female no. 80 was at location 3325 and male no. 48 was at location 3300. On 14 July, the male moved 1900 m downstream to location 1400 and then returned upstream 1920 m to location 3320 on 15 July. On 15 July, the female moved 1920 m downstream to location 1405 and then returned upstream 1907 m to location 3312 on 16 July.

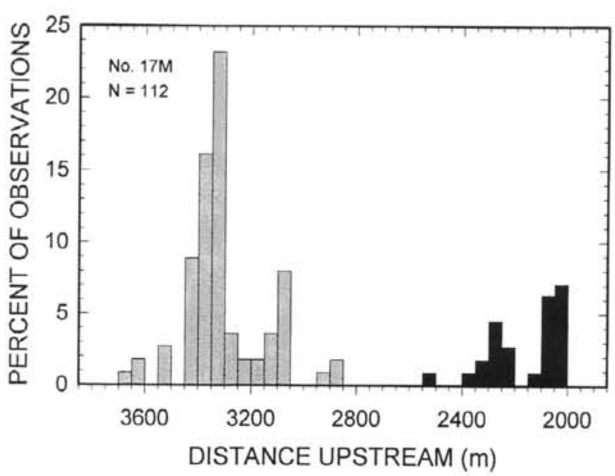

Figure 6. Temporal use of the annual home range of a male *Trionyx spiniferus* in 1995. Shaded bars indicate area occupied 15 May – 6 August, solid bars indicate area occupied 17 April – 14 May. Compare with nos. 46 [1995] and 48 [1995] in Fig. 5.

DISCUSSION

It is likely that several partially interacting variables, including body size and sex (Schubauer et al., 1990), reproductive condition (Yabe, 1992), season (Jones, 1996), and habitat productivity (Brown et al., 1994) could affect home range size in aquatic turtles. In addition, home range size could be affected by habitat type (e.g., lentic or lotic) and the methods used to determine home range size, with telemetry estimates being larger than those determined by mark-recapture (Buhlmann, 1986; Schubauer et al., 1990; Yabe, 1992). Because of the possible influences of habitat and methodology in movement studies of aquatic turtles, we restrict our interspecific comparison of home range parameters of *T. spiniferus* to those species which were studied in lotic habitats using telemetry (Table 2). Home range area for *T. spiniferus* in a small stream is remarkably similar to those for *Chelydra serpentina* and *Trachemys scripta* in small streams (Table 2) and is much smaller than that for *T. muticus* in a large river, despite the fact that *T. muticus* is a closely-related, smaller species (Schubauer et al., 1990). The relationship of home range area and stream width in various species of aquatic turtles (Fig. 7) supports the notion that home range size is also affected by the size of the body of water as suggested by Brown (1967) and Schubauer et al. (1990).

The home range length of *T. spiniferus* in Gin Creek is 2 to 21 times greater than that recorded for other species except that of *Graptemys flavimaculata* in a river (Table 2). In large streams, calculating home range area as length of

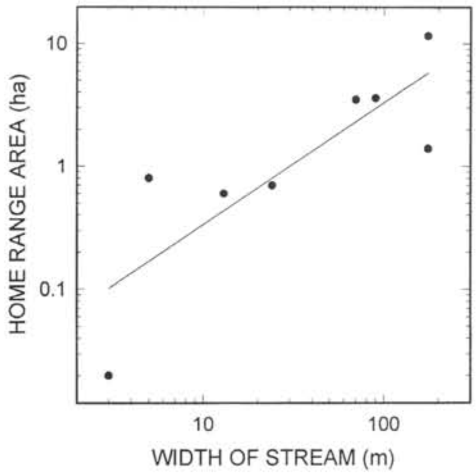

Figure 7. The log-transformed relationship of home range area (y, in ha) and stream width (x, in m) determined from radiotelemetry studies of aquatic turtles in lotic habitats (data from Table 2). The regression equation is $y = 0.034 * x^{0.985}$ ($r = 0.83$, $p = 0.01$).

movement x width of stream may exaggerate the value (e.g., *T. muticus*, Table 2) because a greater proportion of open water habitat may not be used by turtles. For example, most movements of *G. flavimaculata* are restricted to only one side of the river except in narrow channels (Jones, 1996) and movements of *Pseudemys concinna* may be limited to the immediate vicinity of vegetation beds along one side of the river (Buhlmann, 1986). In these cases, the actual measured home range areas for *P. concinna* and *G. flavimaculata* (Table 2) are considerably less than the respective values calculated using stream width (1.4 vs. 6.0 ha and 3.8 vs. 11.9 ha). Similarly, *Trachemys scripta* avoids open water in large streams (Moll and Legler, 1971) and male *T. muticus* in the Kansas River move primarily along the edges of sandbars where they forage on terrestrial arthropods which have fallen into the water (Plummer and Farrar, 1981).

Although statistical significance was not found for any one comparison, male *T. spiniferus* consistently had greater frequency of activity and movement, amount of movement, and home range size than females, a trend similar to that reported for some turtle species (e.g., Schubauer, 1990; Yabe, 1992), but opposite that for *T. muticus* (Table 3).

As with *T. muticus* in a large river, *T. spiniferus* in a small stream made brief long movements out of their home ranges followed by immediate returns. Plummer and Shirer (1975) suggested that such irregular temporary excursions were exploratory in nature and sometimes resulted in shifts in home range location. Rowe and Moll (1991) reported similar excursions in telemetered *Emydoidea blandingii*. The greater frequency of female *T. spiniferus* making long aquatic movements in June and July suggests that such moves were associated with nesting, as in *T. muticus* (Plummer and Shirer, 1975). However, nest sites of *T. muticus* were concentrated on widely disjunct sandbars (Plummer and Shirer, 1975), whereas the five known softshell nest sites on Gin Creek were distributed throughout the length of the study area and were all within 2–3 m of the water. Long movements were not associated with movements to hibernacula (Gibbons et al., 1990) as Gin Creek *T. spiniferus* hibernate within their normal summer home ranges (Plummer and Burnley, 1997; but see Graham and Graham, 1997).

The lack of a clear homing response when *T. muticus* were displaced out of their home ranges caused Plummer and Shirer (1975) to suggest that the displacements may not have been long enough to stimulate homing responses, and other factors also suggested that individual *T. muticus* may have been familiar with the entire > 14 km study area (Plummer, 1977). Because the home ranges of *T. muticus* in Tables 2 and 3 were measured over a relatively short time period (less than a full activity season) compared to each of the other studies in Tables 2 and 3, their sizes, and the conclusions drawn when comparing home ranges between small and large streams, were probably conservative. To render home range sizes of *T. muticus* and *T. spiniferus* more comparable, we recalculated home range lengths for male and female *T. spiniferus* in Gin Creek using only the first 34 days of tracking, as was done for *T. muticus* (Plummer and Shirer, 1975). The recalculated values (males, 1321 ± 55 m; females, 1179 ± 730 m) were not significantly different from the annual home range lengths of *T. spiniferus* in Table 1 (males, $t = 1.52$, $p > 0.10$, df = 12; females, $t = 0.77$, $p > 0.40$, df = 16). Methodologically, however, the values obtained should be more directly comparable to those of *T. muticus* (Table 3).

The likely source of softshell immigrants to Gin Creek was the large population of *T. spiniferus* in the lowest reaches of Deener Creek and the Little Red River ca. 3 km downstream from Gin Creek (Fig. 1). Do the Gin Creek softshells constitute a discrete, functional population? Exactly what constitutes a turtle population is not always easy to discern especially because of terrestrial movements of many aquatic species of kinosternids, chelydrids, and emydids (Gibbons, 1990; Gibbons et al., 1990). Even in highly aquatic species which rarely travel overland, such as trionychids, defining a population can be difficult because of the lack of clear habitat and movement boundaries in large streams (Plummer and Shirer, 1975; Plummer, 1977). Although small in number (< 60 adults, MVP, unpubl. data), the *T. spiniferus* in Gin Creek appear to constitute a discrete, partially isolated, demographically dynamic group rather than just temporary transients from the large Little Red River population downstream. Evidence for this conclusion includes demographic attributes (e.g., equal sex ratio, all age classes represented, high recapture rates; MVP, unpubl.

Table 3. Frequency of daily movement, movement per day, home range length, and area in male and female *Trionyx spiniferus* in a small stream and *T. muticus* in a large river. The values for *T. muticus* are from Plummer and Shirer (1975); home range areas were calculated as in Table 2.

Species	Frequency of Movement (%)		Movement per Day (m/d)		Home Range Length (m)		Home Range Area (ha)	
	m	f	m	f	m	f	m	f
T. spiniferus	88	84	141	122	1756	1420	0.88	0.71
T. muticus	62	75	61	165	474	1228	4.15	21.50

data) and the demonstrated spatial limitation of telemetered turtles. We thoroughly searched the portions of Gin Creek both upstream and downstream from our study area but found no evidence of softshell use.

The large amount of inter-individual variability reported in many of the numerous descriptive studies concerning how aquatic turtles move is interesting because of its possible evolutionary consequences (Gibbons, 1990). A difficult question yet to be answered completely is why do turtles move the way they do? Crucial to understanding the significance of turtle movements is assessing their relative benefits and risks (Bury, 1979; Gibbons, 1990). In this regard, small streams may be advantageous sites for such studies, especially for aquatic species which do not exhibit terrestrial movements, because both the physical environment and turtle populations should be more amenable to manipulation than in large bodies of water. For example, it might be possible in small streams to conduct experimental movement studies involving the alteration of food or nest sites or the manipulation of habitats, predators, or the turtle community composition.

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