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Chapter 7

Structure of an Urban Population of Softshell Turtles (*Apalone spinifera*) Before and After Severe Stream Alteration

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Abstract — We studied a population of softshell turtles (*Apalone spinifera*) in a small urban spring-fed stream (Gin Creek) over a 10-yr period, including before and after a period of major habitat alteration. During habitat alteration (1997–2000), the stream was extensively channelized and the bank cleared of vegetation. Habitat alteration moderately decreased population size but did not greatly affect body size structure or sex ratio. Survivorship of adult turtles marked in 1994–1996 (before habitat alteration) to 2001–2003 (after habitat alteration) was about 10% for males and 25% for females. During the course of the study, about 50% of the adults recruited into the population were previously marked as juveniles; most of the other 50% presumably were new turtles dispersing upstream.

Both radiotelemetric data on movement patterns and mark-recapture data on population structure conducted before habitat alteration suggested that the population was localized and confined to a particular portion of the stream. Radiotracking after habitat alteration demonstrated the ability of turtles to move long distances throughout the drainage system into and out of Gin Creek; however, the proportion of the population that engaged in such movements is unknown. A more comprehensive knowledge of the structure and dynamics of the Gin Creek *A. spinifera* population will require a metapopulation approach that allows estimation of rates of movement in adjacent waters. It appears that *A. spinifera* responds to habitat disturbances in small streams by increasing the rate of long-distance movements. Our data suggest that the Gin Creek population is returning to the structure and behavior that was present before habitat alteration.

Populations of *A. spinifera* are resilient and can persist in urban and suburban environments despite periodic disturbances. Conservation measures for *A. spinifera* and likely other freshwater turtles in small urban streams include maintaining the pool-riffle structure characteristic of small natural streams, maintaining aquatic dispersal corridors to downstream source populations, preserving terrestrial buffer zones adjacent to the stream, and ensuring adequate habitat and survival for all life history stages with an emphasis on measures that reduce the mortality of adults.

Key Words — *Apalone*, Conservation, Habitat Disturbance, Mark-Recapture, Softshell, Survivorship, Turtle, Urban

Because humans dominate Earth's ecosystems, some ecologists (e.g., Collins et al. 2000, Grimm et al. 2000, Alberti et al. 2003, Rosenzweig 2003) have argued that ecological theory must incorporate human activity and behavior to be generally predictive. However, field biologists have traditionally viewed urban areas as "artificial" rather than "natural." Rarely have they established urban study areas or studied urban populations, seeking instead pristine environments that have been impacted little by human activities. Collins et al. (2000) surveyed nine leading ecological journals and found that only 25 of 6157 papers (0.4%) dealt with urban populations; they pointed out the need for ecological studies of populations in urban areas. The current and increasing extent of urbanization hastens ecologists to study the ecology of urban species and use urban species to test the generality of ecological theories developed in more pristine habitats

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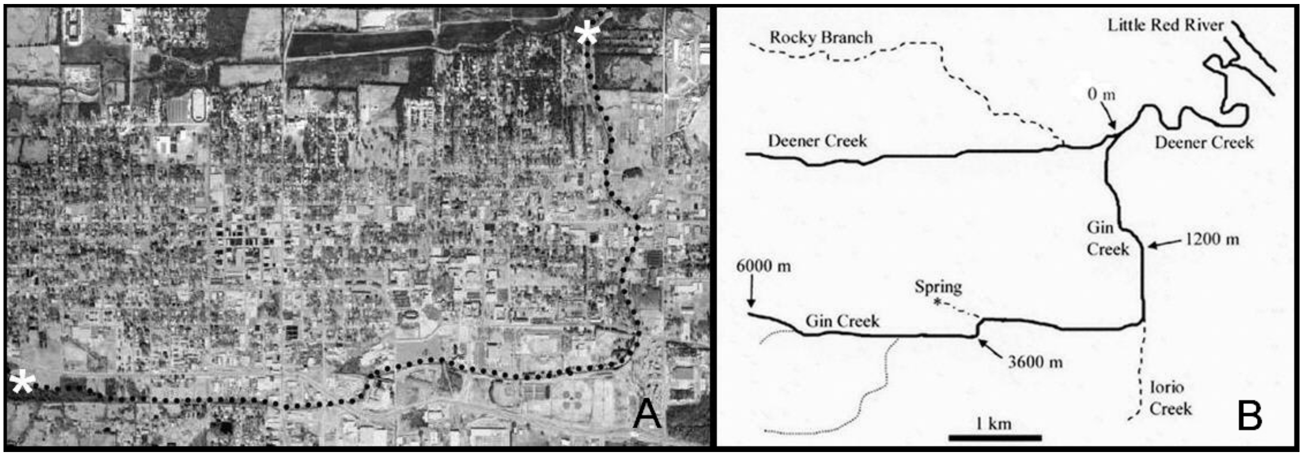

Fig. 1. (A) Aerial photograph of Gin Creek (heavy dotted line) and the urban environment of Searcy, Arkansas. Upper right asterisk indicates mouth (0 m) of stream and lower left asterisk indicates upper end (6000 m) of stream. (B) Map of Gin Creek and larger drainage area. Numbers represent distance (m) upstream from the mouth of Gin Creek. Dashed lines indicate intermittent streams. Dotted lines indicate major drainage ditches. *Apalone spinifera* were normally found in the central portion between locations 1200 and 3600 m.

Our knowledge of the effects of urbanization on animal populations varies greatly among taxonomic groups. For example, urbanization studies are available for rodents (Chernousova 2001), birds (Marzluff 2001), fish (Weaver and Garman 1994), arthropods (McIntyre 2000), macroinvertebrates (Walsh et al. 2001), and mosquitoes (Easton 1994). Declines in richness of algal, invertebrate, and fish communities usually follow stream urbanization (Paul and Meyer 2001). The effects of urbanization on freshwater turtle populations are less well known. Limited studies suggest that some species of turtles seem to be resilient to urbanization and a few may be more abundant in urban areas than they are in more undisturbed environments (Gasith and Sidis 1984; Moll 1980; Moll and Moll 2004).

Studies of freshwater turtle populations in urban environments have the potential to contribute significantly to ecological theory for several reasons: (1) Turtles often maintain high densities and biomass in aquatic communities (Iverson 1982; Congdon et al. 1986) and likely constitute a major component of the community's energy flow and nutrient cycling (Moll and Moll 2004); (2) Repeated anthropogenic disturbances typical of urban streams make them ideal for studying the effect of disturbance (Paul and Meyer 2001) which is thought to be a major contributor to community structure (Menge and Sutherland 1987), and (3) Studies of ecological disturbance require a long-term approach (Magnuson 1995) relative to the taxon of interest (Willig and McGinley 1999) and should incorporate the frequency, extent, and intensity of disturbance (Willig and Walker 1999). Compared to the information gained from studies of short-lived organisms, studies of long-lived turtles subjected to repeated human disturbances consistent with urbanization might provide insight into current models of ecological disturbance (e.g., Walker et al. 1996; Gibbons 1997; Willig and Walker 1999). The accessibility of urban areas may facilitate these long-term studies especially in low-budget research projects. The long-term study reported in this paper grew out of an exercise in an undergraduate ecology laboratory in which biology students conducted much of the fieldwork. The project provided a tangible research experience for undergraduate students greatly facilitated by the proximity, accessibility, and ease of working on a nearby urban stream.

Most urban areas have an extensive network of streams and man-made ditches, canals, and sewers that drain the extensive runoff characteristic of urban areas. Despite the abundance of these lotic habitats in urban areas, studies on the structure and dynamics of freshwater turtle populations in urban lotic habitats are uncommon (e.g., Mitchell 1988; Plummer et al. 1997; Souza and Abe 2000; Rubin et al. 2004; Baldwin et al. 2004; Marchand and Litvaitis 2004; Conner et al. 2005). Additionally, most studies in lotic environments have focused on turtles in rivers rather than small streams (Bury 1979; Moll and Moll 2000, 2004). Because of the rarity of studies in small streams characteristic of many urban areas and because small urban streams may be more unpredictable and subject to greater disturbances (e.g., stagnating, drying, rapid changes in pH, temperature, and nutrient loading; Paul and Meyer 2001) than larger rivers, a need exists for studies of turtle populations in small urban streams.

Our objective is to describe the population structure of Spiny Softshell Turtles, *Apalone spinifera*, in a small urban stream over a 10-yr period that bracketed a stream alteration event. This event greatly altered the habitat physically, but because similar events had occurred in previous decades, the event likely represented a repeated disturbance that temporarily degraded the habitat.

Materials and Methods

Study Species — *Apalone spinifera* is distributed over much of the eastern U.S. west to the Rocky Mountains (Webb 1962).

It is an ecological generalist, being found in a wide variety of lentic and lotic habitats, including disturbed and intermittent habitats associated with human activities, such as borrow pits, drainage ditches, irrigation canals, and small ponds (Webb 1962; Moll and Moll 2004). Despite its extensive distribution, the population ecology of *A. spinifera* is poorly known. With few exceptions, *A. spinifera* is regarded as "common" and is unlikely to attract conservation concern. However, we should be aware of Dodd's (2001, p. 150) caveat regarding the conservation of "common" local species that have been insidiously affected by urbanization (i.e., *Terrapene*), "It is often easier to focus on the needs of exotic wildlife in far-off places than to promote active conservation at home…"

Study Area—Gin Creek is a small, 6 km long, partially spring-fed first order stream in the Little Red River drainage in White County, Arkansas (lat. 35° 15', long. 91° 43'). It is completely enclosed within the town of Searcy (Fig. 1A; population approx. 20,000) and empties into the lower reaches of Deener Creek, which then empties into the Little Red River 3 km downstream (Fig. 1B). Because a spring run feeds Gin Creek 3.5 km upstream from its mouth, the upper 2.5 km of the creek often stagnates or mostly dries during the summer, whereas the lower 3.5 km flows throughout the year (Fig. 1B). Gin Creek receives a large amount of urban runoff from storm sewers, pavement, and other impervious surfaces and provides the major drainage for the southern part of the city (Anonymous 1975; Muncy 1976). Water levels rapidly rise 1–3 m during heavy rains but also rapidly recede afterward. Substrate in the upper 4.8 km of the creek is mostly hard clay, whereas most of the lower 1.2 km is bedrock. Frequent scouring of the creek bed results in unconsolidated sediments being limited to pools, shallow slower waters of inside bends, and small backwater areas created by snags.

Gin Creek has been a prominent landmark in Searcy since establishment of the town in the mid-1800s (Muncy 1976) and probably has been degraded and continuously disturbed since then. A major source of water for Gin Creek is the springs emerging in Spring Park in the center of town (Fig. 1B). In the mid- to late 1800s, these springs were a commercial attraction for tourists who came to Searcy to bathe in the mineral springs (Muncy 1976). The flow rate of the springs has been reduced since that time. There are currently 17 bridges and trestles and one low water dam in the lower 5 km of the stream. Trash and construction materials have been dumped for years at various locations. The stream runs through a portion of the Searcy industrial district and receives various industrial pollutants, including dioxin (Korfmacher et al. 1984) and extensive fertilizer runoff. Major structural modification for flood control, especially channelization, occurred on Gin Creek in the mid-1950s and again in the mid-1970s (Anonymous 1975; Muncy 1976).

Methods — We captured *A. spinifera* mostly by hand (87% of captures) but also with baited 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) or identified it if previously marked, and released it at its capture site. We regularly walked the stream bank searching for basking and nesting sites and observing turtles through binoculars. Selected turtles were brought to the lab to obtain fecal samples for dietary analysis or x-rayed to detect presence/absence of shelled eggs (Gibbons and Greene 1976). Annual data were pooled into three separate 3-yr periods: before habitat alteration (Period 1, 1994–1996), during habitat alteration (Period 2, 1998–2000), and after habitat alteration (Period 3, 2001–2003). Population size represents the actual number of turtles captured during a given period. An individual captured in period N survived to period N+1 only if it was captured in period N+1 or later. Individuals not surviving could have either died or left the study area. A more intensive information-theoretic analysis of survivorship is currently in preparation.

To compare turtle movements with those obtained in 1995–1996, we tracked several turtles intermittently from 1999 through 2002. In May 1999, we captured a large unmarked (445 mm carapace length [CL]; 8 kg) female that apparently had recently dispersed into Gin Creek. Knowledge of her presence was based on the abrupt appearance, several days earlier, of very large dish-shaped depressions characteristically remaining in the substrate when a softshell leaves its buried site. After measuring and marking this large female, we attached a transmitter and tracked her for the next 40 months. Also in 1999, we attached transmitters to five additional adult *A. spinifera* (4 females, 1 male) captured offsite in Deener Creek between the mouth of Gin Creek and the Little Red River. In May 2000, the last year of extensive habitat alteration, we attached transmitters to two adult females captured on the study area and tracked them through August for a thermal ecology study (Plummer et al. 2005).

Data were analyzed with SYSTAT 10.2 (SYSTAT 2002). Unless otherwise stated, means are presented with their standard errors.

Results

We found *A. spinifera* to be limited to the central 2.5 km of Gin Creek (Plummer et al. 1997) probably because substrate in the lower 1.2 km is bedrock and thus does not provide suitable burying sites, and the upper 2.5 km usually stagnates or dries in the summer (Figs. 1, 2). Within the central 2.5 km occupied by softshells, the creek ranges from 2 to 7 m in width (average 4–5 m) and has alternating shallow riffles and deeper pools with a substrate of highly dissected hard clay. At normal summer water levels, depth averages 35 cm and is highly variable over short distances, ranging from <10 cm in riffles to 100 cm in the deeper pools. Beaver (*Castor canadensis*) dams created the largest pools in the creek. Underwater burrows dug into the bank by both Beaver and Muskrat (*Ondontra zibethicus*) provide refugia for *A. spinifera*. Besides softshells, other turtles in Gin Creek include, in relative order of abundance: Sliders (*Trachemys scripta*), Common Musk Turtles (*Sternotherus*

Fig. 2. Habitats along Gin Creek before habitat modification. (A) Creek downstream from central portion inhabited by *A. spinifera*. Note bedrock streambed. (B) Pool habitat in central portion of creek. (C) Riffle habitat in central portion of creek. (D) Creek above the mouth of the spring run and the central portion inhabited by *A. spinifera*. Note isolated pools and drying streambed.

odoratus), Cooters (*Pseudemys concinna*), and Common Snappers (*Chelydra serpentina*). Eastern Mud Turtles (*Kinosternon subrubrum*) have been extirpated within the last 20 yr, likely because of reduction in terrestrial buffer zones along the creek (Burke and Gibbons 1995; Buhlmann and Gibbons 2001; Gibbons 2003; Semlitsch and Bodie 2003).

Gin Creek appears biologically diverse, probably in part due to it being spring-fed (Hubbs 1995). Large-scale fish kills occurred at least five times during the course of our study, some of which were traced to various industrial pollutants. Despite the kills and other repeated apparent degrading situations over several decades, fish (*Fundulus, Lepomis, Micropterus, Ictalurus*, and various cyprinids and catastomids) are abundant, as are clams (*Corbicula, Uniomerus*) and crayfish (*Procambarus clarki* and *P. blandingi*). Crayfish constitute over 80% of the prey items for *A. spinifera* in Gin Creek (M. Plummer unpubl. data).

In 1994, the first year of our study, major activities that altered the stream along a large portion of its length had not occurred for about 20 yr. However, beginning in 1997 and greatly accelerated in 1998–2000, extensive large-scale construction and clearing projects resulted in major structural changes to the stream and stream bank virtually along its entire 6 km length. These projects included road building, exercise trail construction, extensive clearing of bank vegetation, and stream channelization (Fig. 3). Backhoes and bulldozers operated in the streambed itself removing beaver dams, snags, and streamside trees. Impacts on turtles and habitats were striking. For example, we found several softshells that had been crushed by heavy machinery in the streambed and known *A. spinifera* nesting areas that had been covered with gravel and/or concrete. Most of the length of the stream bank had been stripped of vegetation. Because silt fences were not used during construction, the normally clear water was discolored and turbid much of the time, greatly impairing our ability to see and hand-capture turtles. The deepest (1.2 m) pool in the creek, which was heavily shaded by trees along the bank and served as a major refuge for turtles from high summer water

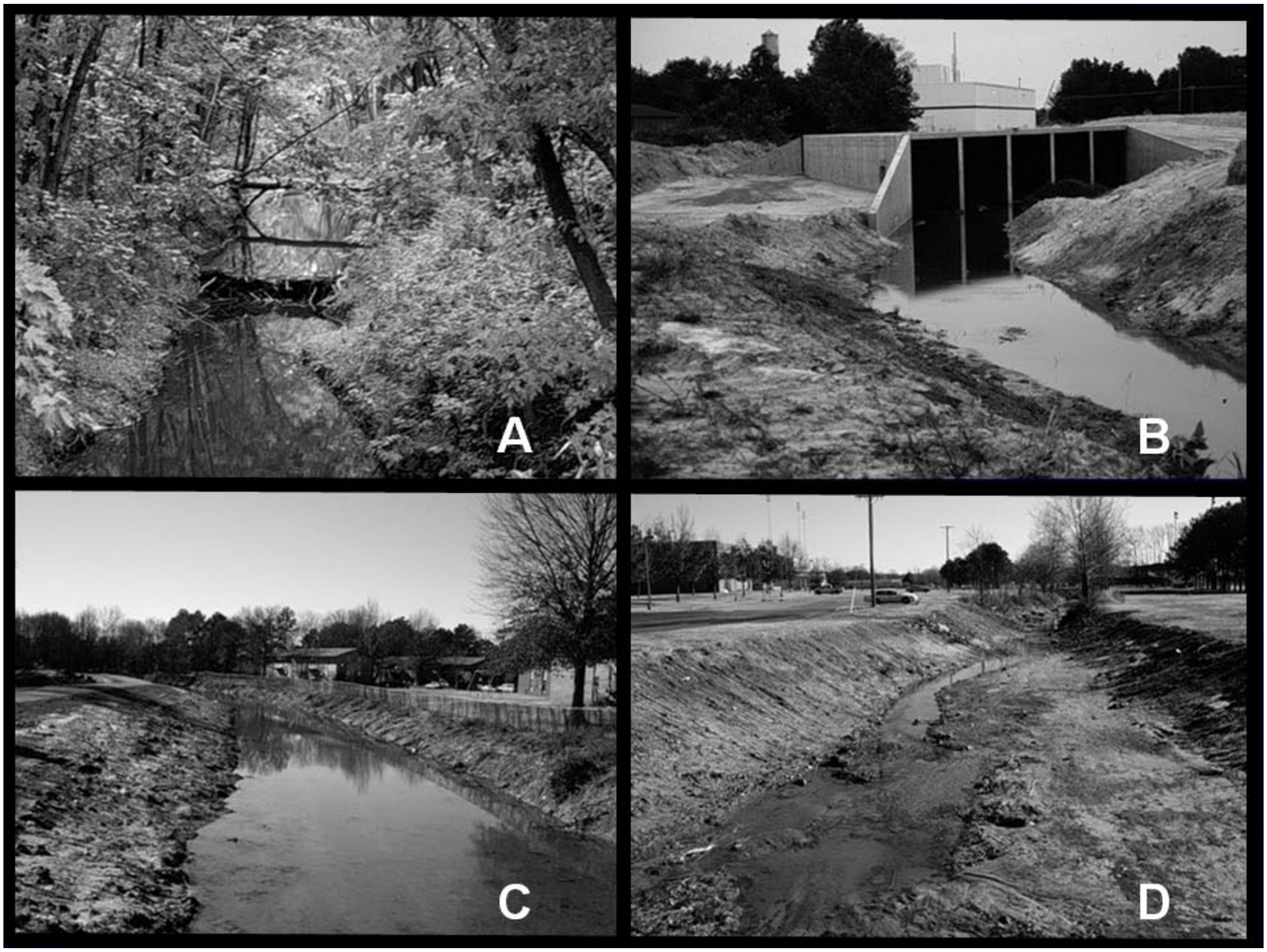

Fig. 3. Habitats along Gin Creek before and after habitat modification. (A) Shaded pool with beaver dam before habitat modification; (B) Same location as "A" after habitat modification. Note bridge construction; (C) Denuded site at a former beaver pool. Note bare stream bank, heavy siltation, backhoe tracks in the streambed, and asphalt exercise trail; (D) Site of a former important summer refuge for turtles, a 1.2 m deep, heavily shaded pool that was reduced to a shallow unshaded ditch less than 25 cm water deep.

temperatures, was completely destroyed by channelization, rendering the stretch uniformly shallow (<20 cm) with little bank vegetation (Fig. 3D).

From 1994–2003, we made 579 captures on 270 individual turtles. Annual sampling effort was not uniform. The number of captures made each year was 27 (1994), 151 (1995), 53 (1996), 25 (1998), 93 (1999), 42 (2000), 18 (2001), 24 (2002), and 117 (2003).

Based on initial capture, adult females were larger ($\bar{x}$ = 229 ± 6 mm PL, 2974 ± 293 g; max. 310 mm, 7800 g, n = 25) than adult males ($\bar{x}$ = 109 ± 2 mm PL, 360 ± 23 g; max. 145 mm, 750 g, n = 48). Gin Creek females measuring at least 190 cm PL contained shelled eggs May–early July and were considered adult. This estimate of size at maturity is consistent with specimens from nearby Tennessee (Robinson and Murphy 1978) and throughout the species' range (Webb 1962). For an estimate of size at maturity for males, we used 90 cm PL (Webb 1962; Robinson and Murphy 1978).

The percent of captured turtles that were previously marked

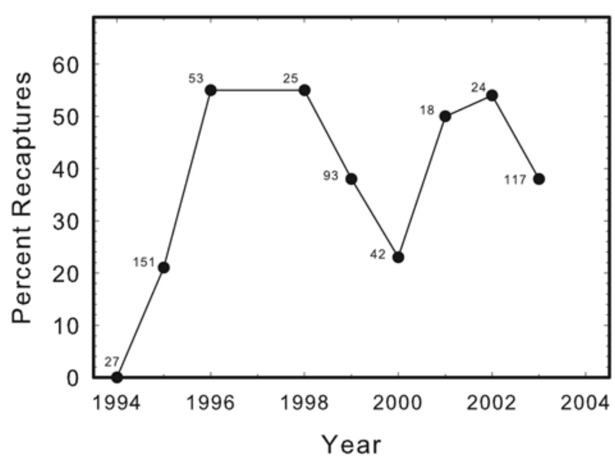

Fig. 4. Percent of recaptures of *Apalone spinifera* each year. Numbers beside symbols indicate the total number of captures for that year. There were no samples taken in 1997.

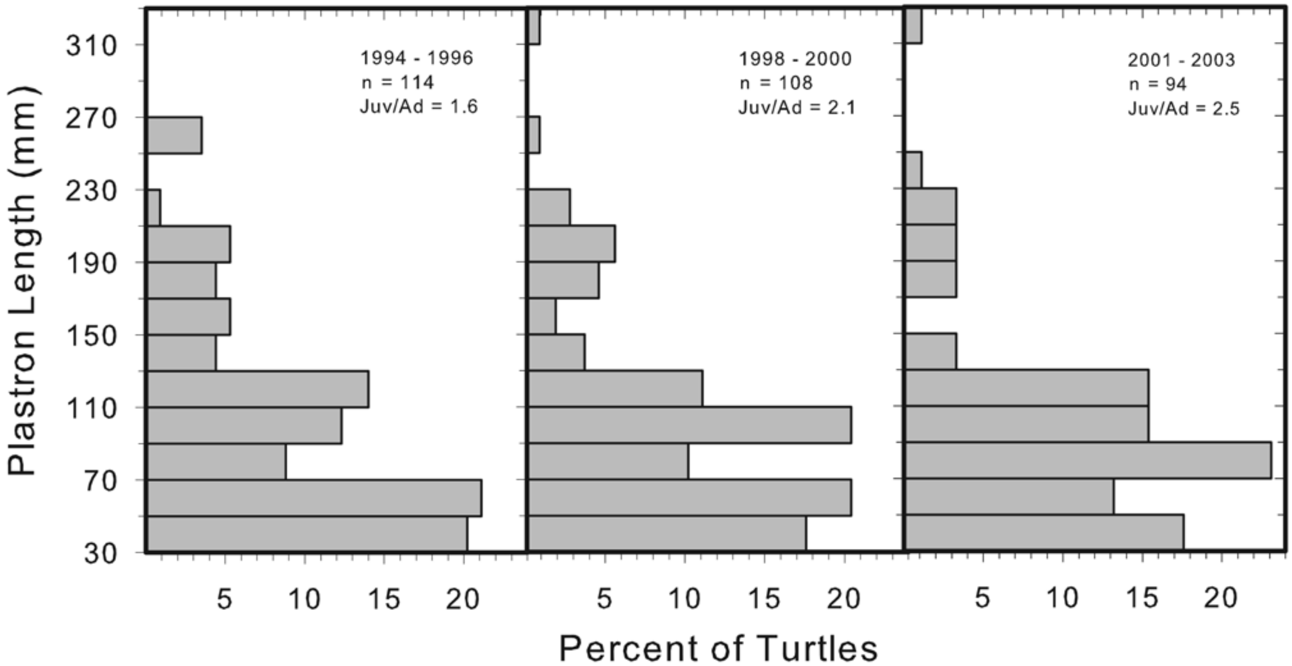

Fig. 5. Body size structure of *Apalone spinifera* in 1994–1996 before habitat modification, in 1998–2000 during habitat modification, and in 2001–2003 after habitat modification. The ratio of juveniles to adults is shown.

rose sharply to about 55% in Period 1 and the beginning of Period 2, decreased sharply to around 20% in Period 2, and then rose to around 40–50% in Period 3 after habitat alteration (Fig. 4). The number of individual turtles captured decreased from 114 in Period 1 to 108 in Period 2 to 94 in Period 3. It is questionable to what extent the decrease in number of individuals captured represents a decrease in actual population size because, especially in Period 2, the rate of recapture was also greatly decreased. A comparison of Periods 1 and 3, more directly comparable with similar rates of recapture, suggests that there may have been a slight decrease in population size.

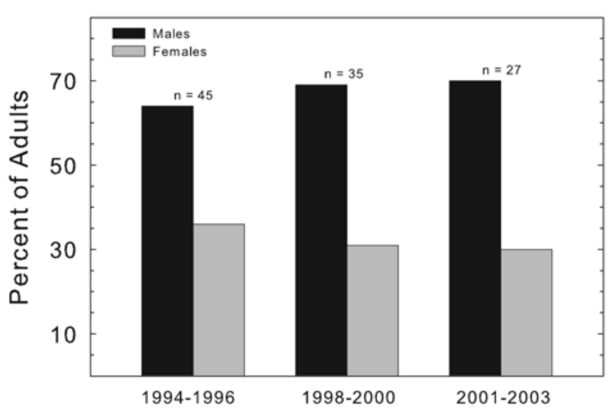

Fig. 6. Sex ratio of adult *Apalone spinifera* before habitat modification (1994–1996), during habitat modification (1998–2000), and after habitat modification (2001–2003). Sample size of adults is indicated above each pair of bars.

Body size structure was similar among the three periods (Fig. 5). Adult sex ratios (M:F) ranged between 2.0 and 2.5:1 and were significantly different from 1:1 in each period (Fig. 6; Period 1, $X^2 = 5.0$, df = 1, P = 0.02; Period 2, $X^2 = 6.4$, df = 1, P = 0.01; Period 3, $X^2 = 4.4$, df = 1, P = 0.04).

Survivorship of turtles marked in 1994–1996 (before habitat alteration) to 2001–2003 (after habitat alteration) was about 5% for juveniles, 10% for adult males and 25% for adult females (Table 1). During the course of the study, 16 of 30 adults recruited into the population (53.3%) were previously marked as resident juveniles; the other half were presumably either new adults dispersing from downstream or resident turtles that had escaped previous capture (Table 2). The rate of recapture for all size classes in 1996–1998 approached 60% (Fig. 4). The overall recapture rate of subadult and adult turtles during the same time was 79% (males 77%, n = 26; females 81%, n = 26). These recapture rates suggest that the probability of new adults being resident turtles that had escaped previous capture was relatively low.

We observed that injured softshells commonly had missing or mutilated limbs and most of the dead turtles found on the study area were missing their heads and limbs. We also found mammalian tooth marks on transmitters, which likely resulted from predators chewing on exposed transmitters that were attached to turtles buried in shallow water. These observations suggest predation by Raccoons (*Procyon lotor*), whose tracks were common on the stream banks and in shallow water areas.

After the disturbance, we tracked the six telemetered turtles captured in Deener Creek in 1999 for 10 periods averaging 84 ± 121 successive days (range 5–362) interspersed with pe-

Table 1. Between-period survivorship of *Apalone spinifera*. Data are the number and percent of survivors/total number of turtles. Period 1 = before habitat modification (1994–1996); Period 2 = during habitat modification (1998–2000); Period 3 = after habitat modification (2001–2003).

	Juveniles		All Adults		Adult Females		Adult Males	
Period	No.	%	No.	%	No.	%	No.	%
1 to 2	16/70	22.9	11/45	24.4	5/16	31.3	6/29	20.7
2 to 3	13/68	19.1	13/35	37.1	4/12	33.3	9/23	39.1
1 to 3	4/70	5.1	7/45	15.6	4/16	25.0	3/29	10.3

riods averaging 275 ± 231 successive days (range 120–783) in which we could not locate the turtles. The movement history of the large 445 mm CL female demonstrates the ability of *A. spinifera* to readily move into and out of Gin Creek. She moved into Gin Creek from downstream at least 4 times in the springs of 4 successive yrs (20 May 1999, 27 April 2000, 17 April 2001, and 20 May 2002). None of the other 5 telemetered turtles moved into Gin Creek but each of them, as well as the large female, moved extensively up and down Deener Creek and the Little Red River. Turtles moved long distances up- and downstream most frequently following heavy rains and high water levels.

Two females tracked in Gin Creek for a thermal ecology study in 2000 eventually left the central study area, moving ca. 900 m upstream. In August, both turtles took refuge in undercut bank burrows in response to the rapidly drying creek characteristic of the upper portion of Gin Creek in late summer (Fig. 2D).

Discussion

Our data must be viewed in context of previously published data on the same population during the early stages of this study. For example, Plummer et al. (1997) found that only four of 1855 daily movements of 16 telemetered adult *A. spinifera* monitored in 1995–1996 occurred outside of the central 2.5 km section of Gin Creek. These four movements occurred during high water after heavy rains and were short-lived; each of the turtles returned to the central area the following day. Individual turtles routinely made long-distance movements to the lower (1200 m) or upper (3600 m) habitat boundaries, only to stop and move in the opposite direction. Plummer et al. (1997) interpreted this as evidence that the *A. spinifera* of Gin Creek existed in a discrete localized population. Mark-recapture data in 1994–1996 supported this parochial view of the population based on a high rate of recapture, an age structure with all age classes represented, and an adult sex ratio marginally different from 1:1. Further, a high juvenile to adult ratio suggested a healthy recruitment of turtles (Gibbs and Amato 2000).

Over the longer-term (10-yr), mark-recapture data, as well as intermittent radiotelemetry data, suggest that movement into and out of Gin Creek appears to be a normal occurrence with varying rates of exchange depending in part on habitat stability. Movements were more restricted after an extended period of habitat stability (e.g., in 1995–1996). The more extensive movements of turtles during the disturbances of 1997–2000 and afterwards combined with the low survivorship and high turnover of turtles suggest a greater rate of exchange. Although it seems clear why a turtle might emigrate from a heavily disturbed area, it is not clear why a turtle might immigrate into such an area from downstream. One possibility is that the detection of upstream disturbances by downstream turtles may stimulate exploratory movements. We did observe increased long-distance movements during heavy rains and high water. Also, each of the movements made by the 445 mm CL female into Gin Creek in 4 successive yrs was too early to be associated with reproduction and the brevity of the movements suggests that they may have been exploratory. Our tracking results demonstrated that adults of both sexes were capable of rapid long-distance dispersal and these are consistent with radiotelemetry studies of *A. spinifera* in rivers flowing into Lake Champlain in Quebec and Vermont where movements up to 25 km have been reported (Graham and Graham 1997; Galois et al. 2002).

Table 2. New adult recruits of *Apalone spinifera* originally marked as resident juveniles in Period 1 and recaptured as adults in Period 2 or marked as juveniles in Period 2 and recaptured as adults in Period 3. Data are the number of resident adult recruits, total number of adult recruits, and percent of resident adult recruits/total new adults.

	Females			Males		
Recapture Period	No. Residents	No. new Adults	Percent	No. Residents	No. new Adults	Percent
2	2	5	40.0	4	12	33.3
3	3	3	100.0	7	10	70.0
Total	5	8	62.5	11	22	59.1

The similarity of population structure (body size, sex ratio, ratio of juveniles to adults) over the course of the study suggests that the rate of movement into the population was similar to the rate of movement out of the population for each sex and body size class. Because males and females use the same microhabitats in Gin Creek (Plummer et al. 1997), it is unlikely that the skewed adult sex ratio in Gin Creek resulted from sampling bias because of sex-specific habitat preferences as occurred in *A. mutica* in a large river (Plummer 1977). Variation in population structure is known to affect recruitment, but it may not immediately result in lower abundance in long-lived organisms like turtles (Marchand and Litvaitis 2004). Demographic shifts in the population structure of freshwater turtles may be associated with degraded habitat (Dodd 1989, 1990; Dodd et al. 1988; Germano and Bury 2001; Marchand and Litvaitis 2004).

Populations of turtles in small urban streams may be particularly vulnerable to both naturally occurring and human-caused habitat alteration because of small population sizes and a greater relative exposure to generalist terrestrial predators. Subsidized predators (i.e., native predators with unnaturally increased abundances due to human activities) are often a major problem for turtle populations in urban areas (Mitchell and Klemens 2000). The Raccoon is often abundant in urban, suburban, and agricultural areas and is considered the single-most important predator on turtles in North America (Mitchell and Klemens 2000). Most mammalian tracks we observed were those of Raccoons, likely the major subsidized predator on *A. spinifera* in Gin Creek, especially on eggs and small turtles. Muskrats are abundant in Gin Creek and may also eat softshells (Parmalee 1989).

We can identify three weaknesses in our study that hinder understanding of the dynamics of the Gin Creek softshell population and its response to habitat alteration: (1) Sampling during the 1998–2000 habitat alteration period may have been inadequate to assess population status. Most turtles were hand captured, but detection and observation of turtles was obscured by water turbidity due to construction activities and erosion. (2) Because we began our study only two years before major habitat alteration began, we lack long-term knowledge on normal population variation when disturbance was minimal. Also, we have little data on normal variation in populations of *A. spinifera* in non-urban areas. Long-term studies of some turtles have demonstrated considerable population variability over time, even in non-disturbed populations (e.g., Congdon and Gibbons 1996). (3) Lastly, our sampling efforts beyond the central 2.5 km portion before habitat alteration may have been inadequate to reject the hypothesis that the population was limited to the central portion. This provincial perception was based on observations that downstream habitats had a bedrock substrate and thus did not provide suitable substrates in which turtles could bury, upstream habitats dried and stagnated in the summer, and movement patterns of individual turtles were highly restricted to the central portion (Plummer et al. 1997). Burke et al. (1995) and Gibbons (1997) argued that to understand the dynamics of turtle populations, biologists must measure population responses to environmental variability with studies that document spatial characteristics of metapopulations. However, most of what is known about the metapopulation dynamics of freshwater turtles has concerned semi-aquatic pond turtles that have the ability for extensive terrestrial dispersal. Based on the extremely high rate of evaporative water loss in *A. spinifera* (Robertson and Smith 1982) and their distinct morphology for an aquatic lifestyle, the ability of softshells to disperse terrestrially is likely minimal (but see Williams and Christiansen 1981). Despite these characteristics, a metapopulation research approach might be fruitful for softshells in streams. For example, a comprehensive understanding of the dynamics of the Gin Creek softshell population will likely require more spatially extensive research that could provide estimates of rates of aquatic movement to and from the downstream populations in Deener Creek and the Little Red River. In July 2001, we caught nine unmarked adult and juvenile *A. spinifera* in a 2 ha pond constructed over 50 yr ago near the 4200 m location on Gin Creek. Because softshells did not normally inhabit this section of Gin Creek and the pond was separated from the creek by a usually dry 75 m long drainage ditch, it is likely that the pond was colonized by softshells moving upstream during high water. Detection of dispersal movements requires a high marking effort and studies of long duration (Burke et al. 1995). Plummer (1977) commented on the difficulty in recognizing the boundaries of populations of *A. mutica* in the Kansas River and concluded that any stream or river "population" of a manageable size for an ecological study may only be a subset of a much larger, ill-defined population in which individuals move freely.

Conservation — Gin Creek is an urban stream that drains a major part of a small town and it will continue to be urbanized and periodically managed for flood control in the future. While it appears that *A. spinifera* populations are fairly resilient and have the capacity to persist in Gin Creek despite periodic habitat disturbance, we would recommend several measures to insure persistence of the softshells (and perhaps the other four species of turtles in the creek). Our recommendations are consistent with those of Bodie (2001) and Moll and Moll (2000, 2004) for the conservation of stream turtles.

(1) Maintain the alternating pool – riffle structure that characterizes most natural small streams. Pools are important refuges for softshells, especially in hot summer months, and provide soft burrowing substrates and benthic macroinvertebrates not found in riffles. Using radiotelemetry, Plummer et al. (1997) found that *A. spinifera* in Gin Creek spent most of their time in pools and relatively little time in riffle areas. Pools also provide overwintering sites for hibernating softshells (Plummer and Burnley 1997).

(2) Maintain dispersal corridors from downstream source populations. Although we have observed *A. spinifera* negotiate beaver dams and natural log and brush jams, large concrete structures (e.g., dams) could hinder movement of this

fully aquatic species. Human activities that prevent normal movements of stream turtles may lead to habitat fragmentation, abnormal population structure, and eventual population decline (Dodd 1990). The importance of maintaining aquatic dispersal corridors for conservation of *A. spinifera* in a large river system has been previously argued (Galois et al. 2002).

(3) Preserve portions of the floodplain that includes the stream channel and bands on each side for passage of the higher velocity flows during floods (Anonymous 1975). Maintaining bank vegetation to shade pools may also be important in these areas. Preserving this space lowers the chance of damage to human structures and also provides terrestrial buffer zones that may be necessary for many herpetofaunal species (Burke and Gibbons 1995; Buhlmann and Gibbons 2001; Gibbons 2003; Semlitsch and Bodie 2003) including essential activities of *A. spinifera* such as basking and nesting (Doody 1995). Preserving wetlands may be futile if adjoining terrestrial areas are not also preserved (Gibbons et al. 2000).

(4) Variability occurs in the sensitivity of different life history stages to population growth among turtle species (Heppell 1998). Although we lack a thorough knowledge of the life history of any *Apalone* species, we would encourage conservation measures that protect all life history stages but focus on those that reduce the mortality of adults. This recommendation is consistent with studies that conclude that effective conservation strategies for turtles focus on measures that increase adult survivorship (Crouse et al. 1987; Congdon et al. 1993, 1994; Heppell et al. 1996).

Addendum — Data collected in 2004 strongly supported conclusions drawn from the 1994–2003 data and further suggested recovery of the Gin Creek population from the 1997–2000 habitat disturbance events. For example, (1) the 2004 recapture rate (64%; 72 captures) was the highest of any year during the study; (2) the adult sex ratio (69% males, 31% females) was identical to that in 2003 (although only 9 of 18 males and 1 of 8 females were captured in both years); (3) population body size structure was similar to that observed in previous periods; (4) survivorship of adults from Period 1 to Period 3 increased sharply when Period 3 was extended to include 2004 (males 10.3% to 34.5%; females 25.0% to 37.5%) suggesting continued return of emigrant adults to the study area. Lastly, (5) we began tracking five adult females captured on the study area in April 2004. By May, three females had left the study area, moving ca. 3000 m downstream into the lower reaches of Deener Creek; one female returned to the study area in July and another returned in September–October. These telemetry results further support the idea of movement into and out of the Gin Creek population from downstream and sharply contrast with the highly restricted movement patterns found in 1995–1996.

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