

## Effects of Habitat Disturbance on Survival Rates of Softshell Turtles (*Apalone spinifera*) in an Urban Stream

MICHAEL V. PLUMMER,<sup>1,2</sup> DAVID G. KREMENTZ,<sup>3</sup> LARKIN A. POWELL,<sup>4</sup> AND NATHAN E. MILLS<sup>1,5</sup>

<sup>1</sup>Department of Biology, Harding University, Searcy, Arkansas 72149, USA

<sup>3</sup>USGS Arkansas Cooperative Fish and Wildlife Research Center, Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 70721, USA; E-mail: krementz@uark.edu

<sup>4</sup>School of Natural Resources, 419 Hardin Hall, University of Nebraska, Lincoln, Nebraska 68583, USA; E-mail: lpowell3@unl.edu

**ABSTRACT.**—We monitored Spiny Softshell Turtles (*Apalone spinifera*) using mark-recapture during 1994–2005 in Gin Creek, Searcy, Arkansas. In 1997–2000 the creek bed and riparian zone were bulldozed in an effort to remove debris and improve water flow. This disturbance appeared to reduce the quantity and quality of turtle habitat. We tested for the potential effect of this habitat disturbance on the survival rates of marked turtles. We estimated annual survival rates for the population using models that allowed for variation in survival by state of maturation, year, and effects of the disturbance; we evaluated two different models of the disturbance impact. The first disturbance model incorporated a single change in survival rates, following the disturbance, whereas the second disturbance model incorporated three survival rates: pre- and postdisturbance, as well as a short-term decline during the disturbance. We used a state-transition model for our mark-recapture analysis, as softshells transition from juveniles to adults in a variable period of time. Our analysis indicated that survival varied by maturation state and was independent of a time trend or the disturbance. Annual survival rates were lower for juveniles ( $\hat{S} = 0.717$ ,  $SE = 0.039$ ) than for adults ( $\hat{S} = 0.836$ ,  $SE = 0.025$ ). Despite the dramatic habitat disturbance, we found no negative effects on survival rates. Our results demonstrate that, like a few other freshwater turtle species known to thrive in urban environments, populations of *A. spinifera* are resilient and can persist in urban environments despite periodic habitat disturbances.

The frequency, extent, and intensity of disturbances are thought to be major contributors to community structure and recruitment (Menge and Sutherland, 1987; Willig and Walker, 1999). The repeated anthropogenic disturbances typical of urban streams make them ideal field sites for studying the effects of disturbance (Paul and Meyer, 2001). The richness of stream communities, notably algal, invertebrate, and fish communities, frequently declines following anthropogenic stream disturbances associated with urbanization (Paul and Meyer, 2001); however, the effects of disturbances on semiaquatic and aquatic tetrapods are less well known. Some species, including some freshwater turtles, may persist following disturbances (Mitchell, 1988; Souza and Abe, 2000; Marchand and Litvaitis, 2004; Conner et al., 2005) and may even be more abundant in urban habitats than they are in more undisturbed natural environments (Moll, 1980; Gasith and Sidis, 1984; Lindeman, 1996; Germano and Bury, 2001). Urban waterways

can provide potential habitat for viable freshwater turtle populations and may be an important component in the conservation of some freshwater species, showcasing wildlife to the public, and promoting conservation (Spinks et al., 2003). However, population characteristics such as sex and age structure, recruitment, and survivorship are largely unknown in urban habitats. Knowledge of these characteristics in urbanized streams is essential if urban streams are to be viewed as a natural resource and appropriately managed, which is often required to ensure that the biological requirements of individual species are met (Spinks et al., 2003).

The Gin Creek drainage in Searcy, White County, Arkansas, exemplifies the network of streams and human-made ditches, canals, and storm sewers that often drain the extensive runoff characteristic of urban areas. Major structural modification for flood control occurred on Gin Creek in the mid-1950s and again in the mid-1970s (Anonymous, 1975; Muncy, 1976). In the mid-1990s, Gin Creek had not experienced major anthropogenic disturbance activities for 20 years. In 1997–2000, extensive construction and clearing projects, including road and bridge building, trail construction, clearing of bank vegetation, and

<sup>2</sup>Corresponding Author. E-mail: plummer@harding.edu

<sup>5</sup>E-mail: nmills@harding.edu

stream channelization, resulted in noticeable structural changes to the stream and stream bank along much of the length of the creek (Plummer and Mills, in press). Construction activities occurred sporadically, unevenly, and simultaneously at multiple areas during these years, but at no time was the entire length of the 6 km creek under construction at the same time. Backhoes and bulldozers operated in the streambed itself removing beaver dams, snags, debris, and streamside trees and woody vegetation. During construction, the normally clear water was often discolored and turbid, especially in 1998. A sizeable portion of the creek's alternating pool and riffle habitat, including a 1.2-m deep pool that served as a major refuge from high summer water temperatures for five species of turtles, was replaced with a uniform depth structure. Habitat disturbance photographs and a more detailed description of the study area may be found in Plummer and Mills (in press).

The Spiny Softshell Turtle, *Apalone spinifera*, was commonly observed in Gin Creek during the decades before the 1990s disturbance. Its presence in Gin Creek was not extraordinary because *A. spinifera* is known to be an ecological generalist that often is found in a wide variety of disturbed and intermittent lentic and lotic habitats associated with human activities (e.g., borrow pits, drainage ditches, irrigation canals, small ponds; Webb, 1962; Moll and Moll, 2004). Furthermore, mark-recapture and radiotelemetric studies beginning in 1994 suggested that the Gin Creek *A. spinifera* population was stable (Plummer and Mills, in press).

To further understand the population structure of *A. spinifera* in Gin Creek, our goal was to use quantitative techniques to determine the effects, if any, of the dramatic 1990s habitat disturbance on survival. Our study's objectives were to (1) use mark-recapture methods to estimate survival rates for softshells during 10 years of monitoring, and (2) use model comparison techniques to assess the impact of the habitat disturbance on survival rates.

#### MATERIALS AND METHODS

**Study Area.**—Gin Creek is a small, partially spring-fed first-order stream (2–7 m in width, up to 1.2 m in depth) in the Little Red River drainage system in White County, Arkansas. An urban stream, its entire 6-km length is included in the town of Searcy. Gin Creek empties into the lower reaches of the larger Deener Creek at a point about 2 km upstream from the mouth of Deener Creek at the Little Red River (see fig. 1 in Plummer and Mills, in press). Because Gin Creek is spring fed approximately 3.5 km

upstream from its mouth, the upper 2.5 km of the creek often stagnates or partially dries during the summer, whereas the lower 3.5 km flows throughout the year. Gin Creek receives a large amount of urban runoff from storm sewers, pavement, and other nonporous surfaces and provides the major drainage for the southern part of the city (Anonymous, 1975; Muncy, 1976). Water levels can rapidly rise 1–3 m during heavy rains but also can fall rapidly afterward.

Previous work demonstrated that *A. spinifera* was primarily limited to suitable habitat in the central 2.5 km of Gin Creek, being isolated from softshells downstream in Deener Creek by a 1.2 km section with an unsuitable bedrock substrate (Plummer et al., 1997; Plummer and Mills, in press). Within this central portion, creek width averages 4–5 m and has alternating shallow riffles and deeper pools with a substrate of highly dissected clay. A large centrally located 1.2-m deep pool shaded by streambank canopy vegetation served as a major refuge for turtles during hot summer days. During the study, there were 17 bridges and trestles and one low water dam in the lower 5 km of the stream. The stream runs through an industrial district and regularly receives various industrial pollutants and fertilizer runoff. Remnants of trash dumps along the creek are evident. Despite more or less continuous disturbance since Searcy's establishment in the mid-1800s (Muncy, 1976), Gin Creek appears to be remarkably biologically diverse, probably in part because of it being spring fed (Plummer and Mills, in press).

**Capture.**—We captured *A. spinifera* during 1994–2005. Most captures (87%) were made by hand in April through June of each year; baited turtle traps supplemented hand captures. For each individual, we determined sex and measured plastron length (PL) and body mass. We gave each animal a unique mark, or identified it if previously marked, and released it at its capture site. Selected turtles were X-rayed for detection of shelled eggs. Each turtle was classified as either a juvenile or an adult. Females measuring >190 mm PL contained shelled eggs from May to early July and were considered adult. This estimate of size at maturity is consistent with Robinson and Murphy (1978) for specimens from nearby Tennessee and Webb (1962) for specimens throughout the species' range. We used 90-mm PL as an estimate of size at maturity for males (Webb, 1962; Robinson and Murphy, 1978).

**Demographic Analysis.**—We used multistate capture-recapture models (Arnason, 1973; Nichols et al., 1992; Williams et al., 2002) to compare annual survival rates among years; we conducted the analysis using program

MARK (White and Burnham, 1999). Although multistate models are often used to estimate transition rates (movements) between geographic strata, we used the models to estimate the transition rate between reproductive states. The modeling process was necessary, because maturation of freshwater turtles from the juvenile ( $j$ , prereproductive) to the adult ( $a$ , reproductive) state is determined largely by reaching a certain body size rather than age (Bury, 1979). As a result, age at maturity is variable and greatly affected by the rate of juvenile growth (Frazer et al., 1990). Although age at maturity for *A. spinifera* has not been determined directly, the combination of variation in body size and growth rates of its sister species, *Apalone mutica* (Plummer, 1977), suggest that maturation in softshells is determined similar to other freshwater turtles. Thus, our model estimated  $\psi_i^{ja}$ , the probability that a juvenile in year  $i$  would become an adult in year  $i + 1$ , given that it survived to  $i + 1$ . Because  $\psi_i^{aj}$ , the probability that an adult would become a juvenile, was not possible, we set  $\psi_i^{aj}$  to zero. We also estimated state-specific annual survival ( $\phi_i^r$ ), the probability of surviving, in state  $r$ , from year  $i$  to year  $i + 1$ , and capture probability ( $p_i^r$ ), the probability that a live turtle in state  $r$  is recaptured during time  $i$ .

Our parameter estimates must be viewed in the context of assumptions that are inherent because of our mark-recapture analyses (Williams et al., 2002). These assumptions include the following: (1) the sample is representative of the population under investigation; (2) there are no marks overlooked or lost; (3) the state of maturation of sampled individuals is correctly determined; (4) survival rates are not affected by marking; (5) marks are correctly recorded; (6) all samples are instantaneous, and release occurs immediately following the sample; (7) all emigration from the sampled area is permanent; and (8) the fate of each turtle with respect to capture and survival probability is independent of the fate of any other turtle. In addition to these traditional mark-recapture assumptions, the multistate approach requires additional assumptions: (1) every marked animal present in state  $r$  at sampling period  $i$  has the same probability ( $p_i^r$ ) of being recaptured; (2) every marked animal in state  $r$  immediately following the sampling in period  $i$  has the same probability of surviving until period  $i + 1$  and moving to state  $s$  by period  $i + 1$  (Williams et al., 2002). The second assumption is different from the standard CJS model in that the multistate model allows variation among turtles in different states but still assumes homogeneity within each state. These transition probabilities reflect a first order Markov process such that only the

previous state at time  $i$  influences the transition to state  $i + 1$ .

The small physical size of Gin Creek usually permitted us the visibility and accessibility to sample all habitats, presumably rendering our sample representative of the population. Biases may have occurred because of observer effects (different field assistants over years) and unequal collection difficulty and effort over the course of the study. For example, frequent water turbidity during the construction years, especially 1998, decreased our ability to see and capture turtles. Because body size at sexual maturation varies among individuals and we used a point value to determine state of maturation, some turtles may have been incorrectly assigned. We occasionally found turtles originally captured and marked in the study area at a collection site in Deener Creek, more than 2 km downstream from the study area. *Apalone spinifera* is known to make long-distance migratory movements in rivers (Graham and Graham, 1997), but it is not known to what extent animals immigrate or emigrate from the Gin Creek population and whether animals that do enter or leave the population do so temporarily or permanently.

Model selection involved two steps. First, we tested our global model, the model in which all the other models are nested, for goodness-of-fit in program RELEASE to generate an estimate of overdispersion of the data ( $c\text{-hat}$ ) (Burnham et al., 1987). Overdispersion (extrabinomial variation) signifies that individuals do not act independently with respect to the survival, movement, and capture processes. Apparent overdispersion can also indicate heterogeneity among individuals, a violation of multistate assumptions (1) and (2) that results in underestimation of sampling variances and covariances (Williams et al., 2002). We used a bootstrap procedure with a Cormack-Jolly-Seber open population recapture model (Cormack, 1964; Jolly, 1965; Seber, 1965) under full-time dependency to test for overdispersion (Burnham et al., 1987), because the bootstrap approach does not work for multistate models. Thus, we pooled maturation states in our analysis of overdispersion. TEST 2 and TEST 3 in program RELEASE yielded a combined  $\chi^2$  of 40.63 ( $df = 33$ ,  $P = 0.16$ ), indicating that overdispersion was not an issue; thus, we made no adjustments to our analyses.

We developed a global model and a series of candidate models to select among (Table 1). The global model included all group and time effects for survival, recapture and transition probabilities for a total of 48 parameters. We then tested a series of models where we constrained group and time effects on each parameter as well as several models where we

TABLE 1. Candidate models used to evaluate variation in survival (S), capture (p), and transition (psi) parameters of Spiny Softshell Turtles in Gin Creek, Searcy, Arkansas.

Model no.	Model structure	Model definition
1	S(constant)p(constant)psi(age)	S and p constant, psi age-dependent
2	S(age)p(age)psi(age)	S, p, and psi all age-dependent
3	S(exp 2, no age)p(age)psi(age)	S differs before and after habitat disturbance but not by age, p and psi age-dependent
4	S(exp 1, no age)p(age)psi(age)	S differs before vs. 3-years after habitat disturbance vs. 7-years after that, p and psi age-dependent
5	S(exp 2*age)p(age)psi(age)	S differs before and after habitat disturbance and by age, p and psi age-dependent
6	S(exp 1*age)p(age)psi(age)	S differs before vs. 3-years after habitat disturbance vs. 7-years after that and by age, p and psi age-dependent
7	S(trap response)p(age)psi(age)	S differs during the first year after capture, p and psi age-dependent
8	S(age)p(time)psi(time)	S age-dependent, p and psi time-dependent
9	S(age*time)p(age)psi(age)	S age- and time-dependent, p and psi age-dependent
10	S(age)p(age*time)psi(age*time)	S age-dependent, p and psi age- and time-dependent
11	S(age*exp 2)p(age*time)psi(age*time)	S differs before and after habitat disturbance and by age, p and psi age- and time-dependent
12	S(age*exp 1)p(age*time)psi(age*time)	S differs before vs. 3-years after habitat disturbance vs. 7-years after that and by age, p and psi age- and time-dependent
13	S(trap response)p(age*time)psi(age*time)	S differs during the first year after capture, p and psi age- and time-dependent
14	S(age*time)p(age*time)psi(age*time)	S(age- and time-dependent)p(age- and time-dependent)psi(age- and time-dependent)

tested for constancy in parameters. Another basic model that we tested was a marking effect model where the first-year survival rate of juvenile softshells was kept constant. This model allowed for a one-year capture or marking effect on juvenile turtles that was constant across all years of the study. Finally, we tested for the effect of habitat disturbance on parameters. We did so in two ways (Table 1). First, we tested three models where the effect of habitat disturbance was short-term (three-year duration), and then the parameters returned to a level that was different than that which occurred before the habitat disturbance was initiated. Next, we tested three models where the effect of habitat disturbance was constant after being implemented (i.e., for the next seven years), but parameters were different than before the disturbance took place.

In designing our models, we had to account for the year when no capture effort was made, 1997. We accomplished this by setting the third time interval of the 10 intervals equal to two. Thus, these parameters represented estimates for the time span of 1996 through 1998.

We considered estimated parameters of interest to be different if the 95% confidence interval of the difference between the parameters did not overlap with zero. The 95% confidence intervals for the difference in parameters were calculated as

$$(\hat{d}_1 - \hat{d}_2) \pm 1.96\sqrt{\text{var}(\hat{d}_1) + \text{var}(\hat{d}_2) - 2\text{Cov}(\hat{d}_1, \hat{d}_2)}$$

We obtained the covariance term from program MARK.

RESULTS

We marked 219 juvenile and 71 adult softshells over 11 years (Table 2). The largest number of turtles caught was 87 during 1995, two years before the habitat disturbance, whereas the smallest number of turtles caught was 16, some five years after the habitat disturbance. The proportion of turtles recaptured the first year after being released ranged from a high of 64% to a low of 12%. The two lowest initial recapture years were 1999 (13%) and 2000 (12%); otherwise there was no apparent pattern. The numbers of turtles recaptured after the first year did not exhibit any real patterns except for the initial cohort captured (1994). That cohort was only recaptured during the first two years possible and then not again. Interestingly, that cohort had the highest initial recapture rate (64%).

TABLE 2. Numbers of softshell turtles released and recaptured by year in Gin Creek, Searcy, Arkansas, between 1994 and 2005. <sup>a</sup>There was no capture effort in 1997, resulting in no captures of previously marked animals.

Release Year	Turtles Released	Recapture Year											Total
		'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	
1994	25	16	2	0 <sup>a</sup>	0	0	0	0	0	0	0	0	18
1995	87		21	0 <sup>a</sup>	5	7	0	0	2	2	2	0	39
1996	42			0 <sup>a</sup>	6	9	2	0	1	0	0	1	19
1997	0 <sup>a</sup>				- <sub>a</sub>	- <sub>a</sub>	- <sub>a</sub>	- <sub>a</sub>	- <sub>a</sub>	- <sub>a</sub>	- <sub>a</sub>	- <sub>a</sub>	- <sub>a</sub>
1998	20					8	2	1	0	2	0	1	14
1999	64						8	3	5	6	3	2	27
2000	42							5	4	2	0	1	12
2001	16								4	3	1	0	8
2002	28									14	3	0	17
2003	73										19	6	25
2004	61											11	11

Model selection indicated that models with maturation state and time effects for both the recapture and state transition parameters had some support, whereas only a state effect was supported for survival (Table 3). The support for time effects, by default, resulted in models with many parameters required. We had hoped that we could model both recapture and state transition in a constrained fashion so that these additional parameters would not have to be estimated and allow the more efficient estimation of survival, the parameter of interest. The model allowing for a trap response received some support but not enough to be considered here. The models that included effects of habitat disturbance, whether long term or not, received little support. In examining the survival rate estimates by maturation state for both of these experimental approaches, the survival estimates varied but not in a pattern consistent with the expected effects of habitat disturbance (Table 4). About the only consistent observation regarding survival was that survival for both adults and juveniles began high, dropped until 1998, increased slightly in 1999, dropped again and finally slowly increased through 2004. Variation around these estimates precludes us from stating these survival rate observations strongly.

We were surprised to also learn that the habitat disturbance was not necessary to model either capture or state transition probabilities. Instead, the most plausible model given the data indicated that only maturation state was necessary to explain survival, capture, and state transition and, also, that time was necessary to explain capture and state transition. The weight for this model, 93%, indicated clearly that this was the best model given the data. In this model, time was not related to the timing of habitat disturbance, but allowed parameters to

vary by year. In general, capture probabilities started high, dropped through period 6 and then rebounded through period 8 (Fig. 1). After that period, juvenile capture probabilities declined, whereas adult capture probabilities remained stable. We caution the reader that our interpretation of the changes in capture probabilities over time should be weighed against the variation around those point estimates (e.g., the initial capture probability had a high point estimate, but the precision of that estimate was poor and, hence, the strength of the observation that capture probabilities declined after the first time may not be clearly supported). Transition probabilities for juvenile to adult were time-specific but the variation around those point estimates was large making any statements about patterns difficult (Fig. 1). Overall, the best-fit models required both capture and state transition parameters to vary across time, but this variation was not related to the episode of habitat disturbance.

Survival rates were state specific and were lower for juveniles than for adults (Table 4). The 95% CI for the difference between these survival rates did not include zero (0.0227–0.2153) which indicated that these survival rates were different.

## DISCUSSION

Our data apparently provide the first estimates of annual survivorship for a trionychid turtle (Iverson, 1991; Shine and Iverson, 1995). Our survival estimates for *A. spinifera* are consistent with the maturation state-specific values reported for various chelydrid, emydid, kinosternid, chelid, and pelomedusid freshwater turtles. For example, juvenile and adult survivorship in *A. spinifera* (0.717, 0.836, respectively) estimated across the entire 11-year study are comparable

TABLE 3. Alternative models for estimation of survival (S), recapture (p), and transition (psi) parameters for Spiny Softshell Turtles in Gin Creek, Searcy, Arkansas, 1994–2005. For each model, time indicates that parameters are time (year) specific, age indicates that parameters are age specific, trap response indicates that there was a one year effect of trapping on turtles, exp 1 indicates that there was a short-term effect (3 yr) of habitat disturbance followed by a survival rate different than before the disturbance, exp 2 indicates that there was a long-term effect (7 yr) of habitat disturbance, and \* indicates an interaction.

Model	AICc	Delta AICc	AICc weights	Model likelihood	No. parameters
{S(age)p(age*time)psi(age*time)}	1119.897	0	0.93085	1	30
{S(age)p(time)psi(time)}	1126.068	6.1712	0.04254	0.0457	20
{S(trap response)p(age*time)psi(age*time)}	1127.502	7.6051	0.02077	0.0223	41
{S(age*exp 2)p(age*time)psi(age*time)}	1130.301	10.4043	0.00512	0.0055	36
{S(age*exp 1)p(age*time)psi(age*time)}	1134.262	14.3653	0.00071	0.0008	38
{S(age*time)p(age*time)psi(age*time)}	1146.193	26.2957	0	0	48
{S(age*time)p(age)psi(age)}	1147.559	27.6614	0	0	23
{S(age*exp 1)p(age)psi(age)}	1149.315	29.4178	0	0	11
{S(age*exp 2)p(age)psi(age)}	1152.56	32.6627	0	0	9
{S(age)p(age)psi(age)}	1153.753	33.8561	0	0	5
{S(trap response)p(age)psi(age)}	1156.235	36.3374	0	0	17
{S(exp 1)p(age)psi(age)}	1158.683	38.7863	0	0	7
{S(exp 2)p(age)psi(age)}	1158.835	38.9376	0	0	6
{S(constant)p(constant)psi(age)}	1165.625	45.7278	0	0	3

to mean survivorship of five species of juvenile freshwater turtles (0.672) and eight species of adult freshwater turtles (0.879; Iverson, 1991). In addition, adult *A. spinifera* survival is comparable with survivorship in a small stream population of *Sternotherus depressus* in a study that employed similar model selection techniques (Fonnesbeck and Dodd, 2003).

Our research bracketed a dramatic disturbance event that could reasonably have been expected to have affected survivorship. Remarkably, we found the disturbance had little effect on survival; in addition, other data indicate that the disturbance had little consequence on other aspects of the population biology of the Gin Creek *A. spinifera* population including population size, size structure, and adult sex ratio (Plummer and Mills, in press). These results suggest that *A. spinifera* may be resilient to stream disturbance in periodically disturbed urban environments over the long term.

We hypothesize that the ability to rapidly move away from and return to the study area was the probable mechanism explaining the lack of effects of the habitat disturbance on the Gin Creek *A. spinifera* population. Based on the recapture information, there might have been a slight drop in numbers of turtles inhabiting Gin Creek in 1999 and 2000 during and immediately after the disturbance; however, our survivorship estimates, recapture rate, and cohort recaptures indicate that the individuals that were not in Gin Creek in 1999 and 2000 apparently did not die. Survival rates did not vary by habitat disturbance period nor did the numbers of individuals recaptured by capture cohort vary by habitat disturbance period. The one exception to the latter observation was the 1994 cohort, which disappeared after 1996. We can offer no explanation for that observation. Thus, we suggest that after dispersing away from the disturbance, turtles survived and slowly returned to the disturbed area.

Our conclusions are consistent with other kinds of data on the Gin Creek *A. spinifera* population. For example, radiotelemetry data demonstrated that less than 1% of daily movements of adults occurred outside the Gin Creek study area in 1995–1996 (Plummer et al., 1997). Each of these movements was followed by an immediate return to the study area and occurred during high water after heavy rains. These movement results combined with concurrent mark-recapture data (e.g., high rate of recapture), all size classes present, and a 1 : 1 adult sex ratio, supported the notion of a discrete stable population in Gin Creek that had limited interchange with downstream populations. However, longer-term mark-recapture and radiotelemetry data suggested that movement into

TABLE 4. Estimates of survival rates, SE and (95% confidence intervals) by age for Spiny Softshell Turtles in Gin Creek, Searcy, Arkansas, 1994–2005. Disturbance effect A = effect of habitat disturbance was short-term, three-year duration, and then the parameters returned to a level that was different than occurred before the habitat disturbance was initiated. Disturbance effect B = effect of habitat disturbance was constant after being implemented (for the next seven years), but parameters were different than before the disturbance took place.

	Group	Model		
			Disturbance effect A	Disturbance effect B
Ad	0.836 ± 0.0249 (0.7811–0.8790)	Before	0.801 ± 0.089 (0.5713–0.9239)	0.801 ± 0.0899 (0.5714–0.9239)
		During	0.901 ± 0.1378 (0.3040–0.9948)	
		After	0.809 ± 0.1035 (0.5327–0.9408)	0.853 ± 0.0376 (0.7633–0.9127)
Juv	0.717 ± 0.0389 (0.6352–0.7869)	Before	0.693 ± 0.1559 (0.3492–0.9047)	0.693 ± 0.1559 (0.3492–0.9047)
		During	0.692 ± 0.1019 (0.4683–0.8516)	
		After	0.554 ± 0.1039 (0.3525–0.7388)	0.627 ± 0.0595 (0.5054–0.7347)

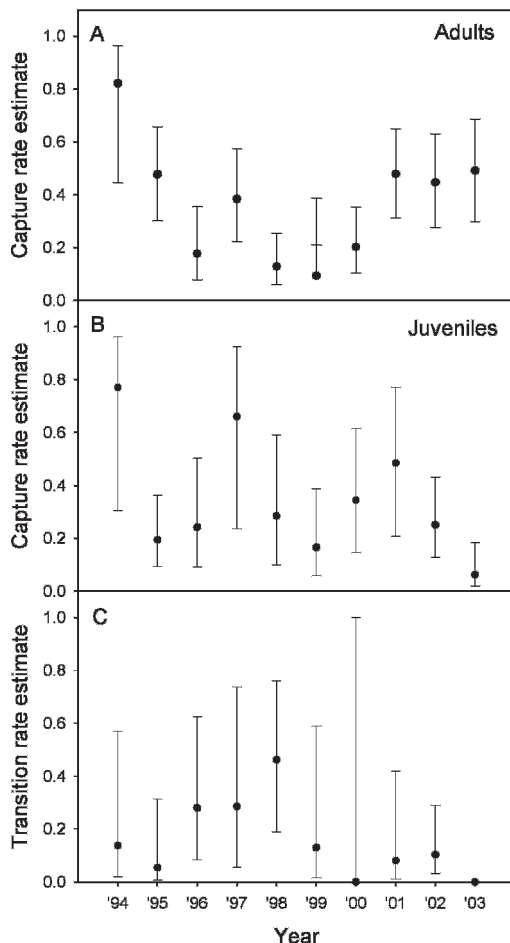


FIG. 1. Capture rate (A) adults, (B) juveniles, and transition (C) probabilities for juvenile and adult *Apalone spinifera* in Gin Creek over 10 years. Error bars represent 95% confidence intervals.

and out of Gin Creek was a normal occurrence with exchange rates depending in part on the extent of habitat stability (Plummer and Mills, in press). Similarly, in box turtles (*Terrapene carolina*), major disturbance events did not affect survival rates providing the turtles could disperse to relatively undisturbed favorable habitat to wait out the disturbance (Dodd et al., 2006).

A more complete understanding of the dynamics of the Gin Creek *A. spinifera* population and the importance of the availability of dispersal corridors will require a carefully designed long-term study that incorporates both dispersal and metapopulation concepts (Burke et al., 1995; Gibbons, 1997). This study would require a high marking and recapturing effort both in Gin Creek and in surrounding habitats that may provide refuge. Previous studies with this geographic extent have demonstrated that considerable population variability may exist over time in both undisturbed (Congdon and Gibbons, 1996) and disturbed (Dodd et al., 2006) populations of turtles.

Small populations of freshwater turtles in streams would seem to be particularly vulnerable to habitat destruction or disturbance. Human activities that prevent normal movements of turtles in streams may lead to habitat fragmentation, decreased survival, abnormal population structure, and eventual population decline (Dodd, 1990). However, our data from Gin Creek indicate that the simple act of maintaining dispersal corridors to and from downstream populations during a disturbance may diminish the effects of habitat disturbance by providing turtles escape from the short-term dangers of disturbance. Physically escaping disturbance may allow long-term survival of individual turtles and ultimately survival of turtle popula-

tions even in the highly modified habitats common in urban areas.

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#### LITERATURE CITED

- ANONYMOUS. 1975. Flood Plain Information: Little Red River and Tributaries, Searcy, Arkansas. Report U.S. Army Corps of Engineers, Little Rock, AR.
- ARNASON, A. N. 1973. The estimation of population size, migration rates, and survival in a stratified population. *Researches on Population Ecology* 15:1–8.
- BURKE, V. J., J. L. GREENE, AND J. W. GIBBONS. 1995. The effect of sample size and study duration on metapopulation estimates for Slider Turtles (*Trachemys scripta*). *Herpetologica* 51:451–456.
- BURNHAM, K. P., D. R. ANDERSON, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5:1–437.
- BURY, R. B. 1979. Population ecology of freshwater turtles. In M. Harless and H. Morlock (eds.), *Turtles: Perspectives and Research*, pp. 571–602. Wiley-Interscience, New York.
- CONGDON, J. D., AND J. W. GIBBONS. 1996. Structure and dynamics of a turtle community over two decades. In M. L. Cody and J. A. Smallwood (eds.), *Long-Term Studies of Vertebrate Communities*, pp. 137–159. Academic Press, San Diego, CA.
- CONNER, C. A., B. A. DOUTHITT, AND T. J. RYAN. 2005. Descriptive ecology of a turtle assemblage in an urban landscape. *American Midland Naturalist* 153:428–435.
- CORMACK, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- DODD, C. K., JR. 1990. Effects of habitat fragmentation on a stream-dwelling species, the Flattened Musk Turtle, *Sternotherus depressus*. *Biological Conservation* 54:33–45.
- DODD, C. K., JR., A. OZGUL, AND M. K. OLI. 2006. The influence of disturbance events on survival and dispersal rates of Florida Box Turtles. *Ecological Applications* 16:1936–1944.
- FONNESBECK, C. J., AND C. K. DODD. 2003. Estimation of Flattened Musk Turtle (*Sternotherus depressus*) survival, recapture, and recovery rate during and after a disease outbreak. *Journal of Herpetology* 37:602–607.
- FRAZER, N. B., J. W. GIBBONS, AND J. L. GREENE. 1990. Life tables of a Slider Turtle population. In J. W. Gibbons (ed.), *Life History and Ecology of the Slider Turtle*, pp. 183–200. Smithsonian Institution Press, Washington, DC.
- GASITH, A., AND I. SIDIS. 1984. Polluted water bodies, the main habitat of the Caspian terrapin (*Mauremys caspica rivulata*) in Israel. *Copeia* 1984:216–219.
- GERMANO, D. J., AND R. B. BURY. 2001. Western pond turtles (*Clemmys marmorata*) in the Central Valley of California: status and population structure. *Transactions of the Western Section of the Wildlife Society* 37:22–36.
- GIBBONS, J. W. 1997. Measuring declines and natural variation in turtle populations: spatial lessons from long-term studies. In J. van Abbema (ed.), *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference*, pp. 243–246. New York Turtle and Tortoise Society, New York.
- GRAHAM, T. E., AND A. A. GRAHAM. 1997. Ecology of the eastern spiny softshell, *Apalone spinifer spinifer*, in the Lamoille River, Vermont. *Chelonian Conservation and Biology* 2:363–369.
- IVERSON, J. B. 1991. Patterns of survivorship in turtles (order Testudines). *Canadian Journal of Zoology* 69:385–391.
- JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and dilution-stochastic model. *Biometrika* 52:225–247.
- LINDEMAN, P. V. 1996. Comparative life history of Painted Turtles (*Chrysemys picta*) in two habitats in the inland Pacific Northwest. *Copeia* 1996:114–130.
- MARCHAND, M. N., AND J. A. LITVAITIS. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. *Conservation Biology* 18:758–767.
- MENGE, B. A., AND J. P. SUTHERLAND. 1987. Community regulation: variation in disturbance, competition, and predation in relation to gradients of environmental stress and recruitment. *American Naturalist* 130:730–757.
- MITCHELL, J. C. 1988. Population ecology and life histories of the freshwater turtles *Chrysemys picta* and *Sternotherus odoratus* in an urban lake. *Herpetological Monographs* 2:40–61.
- MOLL, D. 1980. Dirty river turtles. *Natural History* 89:42–49.
- MOLL, D., AND E. O. MOLL. 2004. *The Ecology, Exploitation, and Conservation of River Turtles*. Oxford University Press, New York.
- MUNCY, R. L. 1976. *Searcy, Arkansas: A Frontier Town Grows Up With America*. Harding Press, Searcy, AR.



- NICHOLS, J. D., J. R. SAUER, K. H. POLLOCK, AND J. B. HESTBECK. 1992. Estimating transition probabilities for stage-based population projection matrices using capture-recapture data. *Ecology* 73:306–312.
- PAUL, M. J., AND J. L. MEYER. 2001. Streams in the urban landscape. *Annual Review of Ecology and Systematics* 32:333–365.
- PLUMMER, M. V. 1977. Reproduction and growth in the turtle *Trionyx muticus*. *Copeia* 1977:440–447.
- PLUMMER, M. V., AND N. E. MILLS. In press. Structure of an urban population of softshell turtles (*Apalone spinifer*) before and after stream alteration. In R. E. Jung and J. C. Mitchell (eds.), *Urban Herpetology*. Herpetological Conservation. Vol. 3. Society for the Study of Amphibians and Reptiles. Salt Lake City, UT.
- PLUMMER, M. V., N. E. MILLS, AND S. L. ALLEN. 1997. Activity, habitat, and patterns of movement of softshell turtles (*Trionyx spiniferus*) in a small stream. *Chelonian Conservation and Biology* 2:514–520.
- ROBINSON, K. M., AND G. G. MURPHY. 1978. The reproductive cycle of the eastern Spiny Softshell Turtle (*Trionyx spiniferus spiniferus*). *Herpetologica* 34:137–140.
- SEBER, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- SHINE, R., AND J. B. IVERSON. 1995. Patterns of survival, growth and maturation in turtles. *Oikos* 72:343–348.
- SOUZA, F. L., AND A. S. ABE. 2000. Feeding ecology, density and biomass of the freshwater turtle, *Phrynops Geoffroanus*, inhabiting a polluted urban river in south-eastern Brazil. *Journal of Zoology* London 252:437–446.
- SPINKS, P. Q., G. B. PAULY, J. J. CRAYON, AND H. B. SHAFFER. 2003. Survival of the western pond turtle (*Emys marmorata*) in an urban California environment. *Biological Conservation* 113:257–267.
- WEBB, R. G. 1962. North American recent soft-shelled turtles (family Trionychidae). University of Kansas Publications, Museum of Natural History 13:429–611.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. *Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making*. Academic Press, San Diego, CA.
- WILLIG, M. R., AND L. R. WALKER. 1999. Disturbance in terrestrial ecosystems: salient themes, synthesis, and future directions. In L. R. Walker (ed.), *Ecosystems of Disturbed Ground*, pp. 747–767. Elsevier Science, Amsterdam, The Netherlands.

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