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Author(s): Francis L. Rose and Michael F. Small
Source: The Southwestern Naturalist, 59(3):331-336.
Published By: Southwestern Association of Naturalists
https://doi.org/10.1894/NBF-08.1
URL: http://www.bioone.org/doi/full/10.1894/NBF-08.1

POPULATION SIZE, SURVIVORSHIP, DENSITY, AND CAPTURE PROBABILITY OF *CHELYDRA SERPENTINA* INHABITING AN URBAN ENVIRONMENT

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ABSTRACT—We conducted a mark-recapture study on snapping turtles (*Chelydra serpentina*) at the headwaters of the San Marcos River, Hays County, Texas. The site is within a highly modified urban environment partially surrounded by a golf course, athletic fields, remnants of a theme park, and roadways supporting high traffic volume. We conducted the study from 1996–2011. We captured 179 turtles (89 adult females, 77 adult males, and 13 juveniles). We recaptured males significantly more frequently than females. We estimated population size to be 215 individuals with a density of 26/ha. The annual estimated probability of capture was 0.33, and estimated annual survivorship was 0.94 for males, 0.93 for females, and 0.81 for juveniles.

RESUMEN—Se realizó un estudio de marca-recaptura de tortugas mordedoras (*Chelydra serpentina*) en la cabecera del río San Marcos, el condado de Hays, Texas. El lugar se encuentra dentro de un ambiente urbano altamente modificado, rodeado parcialmente por un campo de golf, campos de atletismo, remanentes de un parque temático y autopistas con tráfico de alto volumen. Este estudio se llevó a cabo de 1996 hasta 2011 y en este período de tiempo se capturaron 179 tortugas (89 hembras adultas, 77 adultos machos y 13 juveniles). El número de machos recapturados fue significativamente mayor que el de las hembras. El tamaño estimado de la población fue de 215 individuos con una densidad de 26/ha. La probabilidad anual estimada de captura fue de 0.33, y la probabilidad anual estimada de sobrevivencia fue de 0.94 para los machos, 0.93 para las hembras y 0.81 para los juveniles.

The risks that increased urbanization pose to wildlife are challenging problems for conservation biologists (McKinney, 2002; Foley et al., 2012). Particularly at risk are species with limited ability to adapt to these changes either through modifying behavior or physically relocating to more suitable habitats. Species that rely on movement patterns such as dispersal and migration are often negatively impacted as their passageways are disrupted (Doak et al., 1992; Collingham and Huntley, 2000; Nour et al., 1993). Additionally, species may become more vulnerable to predation as they become isolated. This often results in an increase in mesopredators (Wilcove, 1985; Prange et al., 2004), thus disrupting established predator-prey interactions (Kaveiva, 1987). Researchers have already attributed cases of reduction in species richness and population size to urbanization in the United States (Dickman, 1987; McKinney, 2002).

Freshwater turtles inhabiting urban environments may be negatively impacted in several ways. Fragmented habitats pose challenges regarding seasonal terrestrial movements associated with reproduction (Baldwin et al., 2004), and some turtles avoid habitats where they encounter human activity (Ryan et al., 2008). Some turtles travel increased distances searching for suitable nesting sites, exposing them to increased mortality from vehicles (Haxton, 2000; Steen and Gibbs, 2004; Gibbs and Steen, 2005) and predators (Congdon and Gatton, 1989), as well as potentially altering tertiary sex ratios. In addition, females might not be able to construct nests in sites that afford maintenance of secondary sex ratios (Janzen, 1994). Restrictions in nesting sites might result in higher local nest densities, favoring predation by mesopredators (Burke et al., 1998; Marchland and Litvaitis, 2004; Prange et al., 2004).

Golf courses may provide suitable nesting habitat for freshwater turtles because some turtle species readily use open areas to nest (Failey et al., 2007; Colding et al., 2009; Harden et al., 2009). However, golf course managers routinely use pesticides, herbicides, and fungicides (Rodewald et al., 2005; Colding et al., 2009) for grounds maintenance and these substances have been shown to accumulate in golf course ponds. How these accumulated chemicals impact food quality and turtle life history traits is unknown.

Several authors addressed survivorship of adult snapping turtles (*Chelydra serpentina*; Hammer, 1969; Obbard and Brooks, 1980; Galbraith and Brooks, 1987; Congdon et al., 1994; Flaherty et al., 2008). The annual estimated survival for adults ranged from 75–96%. Mean annual estimated survivorship increased with size and age (Congdon et al., 1994; Heppell, 1998). Heppell (1998) found hatchlings to have annual survival rates of 6.6–23.0%, and this increased to 67.8% for 1–6 y, 75.5% to 9 y, 80.7% from 7–12 y, and 75.4% between 10–18 y, whereas adults had an estimated survivorship of 94.0–96.6%. Congdon et al. (1994) estimated annual survivorship of juvenile *C. serpentina* in Michigan exceeded 65% at age 2, and reached 77.0% from 2–12 y. Adult females in Ontario had an estimated average annual survivorship of 96.6% (13-y mean; Brooks et al., 1991; Galbraith and Brooks, 1987).

Flaherty et al. (2008) used a data set generated over 17 y and approached estimated survivorship from a management perspective related to harvesting. They estimated annual survivorship at 97% for their population in Canaan Valley, West Virginia, although the authors stated that their use of single-door traps might have affected the capture of small and large individuals.

Chelydra serpentina has the broadest geographic range of any North American chelonian (Iverson, 1992). Although adults are large, frequently numerous in aquatic settings, and easily trapped and marked, there are few published comprehensive life-history studies of this species in the southern portion of its range (see Moll and Iverson, 2008 for a comprehensive review) and none in Texas (see Dixon, 2000).

Texas State University purchased Spring Lake in 1994 to add to its contiguous main campus. The stated goals of the property purchase were to enhance research, education, and community outreach. A mark-recapture study of turtles was begun at the site in 1996 (Rose, 2011). As of December 2011, researchers have marked over 4,000 individuals of the four primary species: *C. serpentina*, Texas river cooter (*Pseudemys texana*), red-eared slider (*Trachemys scripta elegans*), and stinkpot (*Sternotherus odoratus*). Systematic capture regimes over 15 y provided data sets that allow evaluation of various life history traits and behaviors. The large number of captures and recaptures of *C. serpentina* provided a substantial data set that allowed us to estimate population size, male and female survivorship, and densities, and to determine if biases occurred in the sex ratio.

Materials and Methods—*Study Area*—Approximately 200 springs emerge from the Edwards Aquifer to form the headwaters of the San Marcos River in Hays County, Texas. San Marcos Springs is the second largest spring system in Texas with an average flow rate of 4.8 cms or 47,142 kL/d. The 600-m spring-run was dammed in 1849 (Fields et al., 2003) to form Spring Lake and a lentic slough. The slough (100 m across at its confluence) is the terminal drainage basin for Sink Creek, the only surface input into the lake. Surface area of the aquatic portion (lake and slough) is 8.1 ha, and the combined length of the lake and slough is 1.6 km. Although the water temperature is consistent (22 ± 2°C) in the lake, it varies with season in the slough. Because of the high flow rates, the lake has little bottom sediment, but the slough has a thick layer of mud and organic debris, numerous logs, and emergent and aquatic vegetation. The eastern shore of the lake is bordered by rock and concrete walls and the western edge by the Balcones Escarpment. A golf course, which has been in existence for over 80 y (Watkins, 1930), and intramural athletic fields border the slough. The property (36 ha) is bordered on all sides by roadways and is transected by a high-traffic road where turtles may be killed during the spring-summer nesting period. The resulting configuration of the site is a highly modified terrestrial environment surrounded by roads, containing a continuously flowing spring-fed lake with a lentic slough, and bordered by a golf course and athletic fields.

The springs in the lake provide continuous flow that may reach significant levels; however, the slough serves as a water source during floods, with large volumes of water sequestered from its 122.6-km^2 runoff area. Severe floods occurred during our study in 1998, 2001, 2002, and 2007. The 1998 flood was the most severe when 510–760 mm of rain fell within 24 h, causing water to purge the system. Rushing water felled trees, churned bottom sediments of the slough and, altered its configuration, and swept away brush and aquatic vegetation leaving vast piles of detritus when the water receded. Researchers found dead turtles, mostly *Sternotherus odoratus*, within these piles but noted no snapping turtle carcasses. One shell of an unmarked snapping turtle was found protruding from the mud in the slough 6 mo after the flood. How turtles in general, and snapping turtles in particular, navigate such floods is not understood, but we noticed no significant reduction in the number of marked individuals of either species.

Trapping—We captured snapping turtles with hoop traps, with dip nets, and by hand. Three times (May, July, November) each year (1996–2011), we set six–eight traps along a segment of the slough and lake. We left the traps in place for 4 d, then moved them for a combined 16 d. We checked traps every 3 h during the day and at 2000h and again at 0700h the following day. Traps had a single throat and were composed of three metal rings, 78.7 cm in diameter, with nylon mesh that formed a 3.8-cm square when the trap was set. We baited the traps with fish, chicken, and various meats hung in a 12.7 × 13.9 × 5-cm metal mesh (1-cm) frame to thwart easy access. Trapping times were consistent over the trapping periods and totaled 138,240 trap hours. In addition to capturing snapping turtles in traps, we also routinely dip-netted, or hand-caught throughout the years as part of other studies.

We measured (carapace and plastron lengths) and weighed captured turtles and placed a passive integrated transponder tag subcutaneously at the dorsal base of the tail of each turtle. In addition, we engraved a number into the first vertebral scute. The combination of the two identifying methods allowed us to identify carcasses of marked individuals. Sex was determined following protocol established by Mosimann and Bider (1960) and by observation of the presence or absence of a penis while the turtle was being handled. We have not ascertained the size at which male and female *C. serpentina* become sexually mature, so we considered juveniles to have carapace lengths less than 200 mm (mean was 79 mm, range 45–188 mm).

Following initial capture, we released turtles at their point of capture within 2 h. For subsequent captures, we released turtles within 10 min.

Table 1—The eight competing models, ordered from best to worst fit, used to estimate population size, survivorship, and probability of capture for *Chelydra serpentina* in Spring Lake, Aquarena Center, San Marcos, Texas.

Model[a]	AICc	ΔAICc	AICc weight	No. of parameters
ϕ(g)p(.)pent(.)*N*(g)	1846.1412	0.0000	1.0000	8
ϕ(g)p(.)pent(.)*N*(.)	44,320.7067	42,474.5555	0.0000	6
ϕ(.)p(g)pent(.)*N*(.)	82,328.7187	80,482.5675	0.0000	6
ϕ(g)p(g)pent(.)*N*(g)	99,487.2592	97,641.1080	0.0000	10
ϕ(.)p(.)pent(.)*N*(g)	99,495.4457	97,649.2945	0.0000	6
ϕ(g)p(g)pent(.)*N*(.)	99,500.8318	97,654.6806	0.0000	8
ϕ(.)p(.)pent(.)*N*(.)	99,527.6427	97,681.4915	0.0000	4
ϕ(.)p(g)pent(.)*N*(g)	Failed to reach numerical convergence.			

[a] Abbreviations: AICc = Akaike's information criterion with a correction for small sample size; ϕ = survivorship; p = probability of capture; pent = probability of entry into the population; *N* = population size; (g) = a grouping variable for sex-age; (.) = constancy over time.

Parameter Estimation—We estimated population size, apparent survivorship, and probability of capture for adult male, adult female, and juvenile snapping turtles using the POPAN data type algorithm with a sine link function in Program MARK (White and Burnham, 1999) and second-part variance estimation procedures with 16 1-y time-steps to derive our estimates with associated 95% confidence intervals. The POPAN data type in MARK emulates a parameterized Jolly-Seber model that is highly robust and found in the stand-alone program POPAN-5 (Schwarz and Arnason, 1996).

We ran eight competing models (seven models ran successfully whereas one failed to reach numerical convergence) including from 4–10 parameters to determine estimated population size, estimated survivorship, estimated probability of capture, and probability of entry into the population (Table 1). Because our primary interests were estimated population size, estimated probability of capture, and estimated apparent survivorship for sex-age categories, we used the grouping variables to indicate if a model calculated separate estimates for each age-sex category and (.) indicating group independence. We set the models to run with probability of entry into the population group independent [i.e., (.)]. The best-fit model to the data was determined using Akaike's information criterion with a correction for small sample size methodology (Table 1; Burnham and Anderson, 2002).

We used mass at first capture of the 20 largest of each sex to ascertain whether there were gender differences in size. This eliminated the concern of using all individuals because we did not know the size at which maturation occurred (Gibbons, 1970). The results are expressed in millimeters as the mean ± SD *(data range)*.

Results—We captured 179 *C. serpentina*; 89 (49.7%) were adult females, 77 (43.0%) were adult males, and 13 (7.3%) were juveniles. The sex ratio (1.1:1 female:male) did not differ significantly from equality ($\chi^2_1 = 0.86$, $P < 0.3517$). We recaptured males (404 times) more frequently than females (279 times; $\chi^2_1 = 22.78$, $P < 0.001$).

The 20 largest males attained a mean carapace length of 338 ± 17.8 (318–383) and were significantly ($t_{38} = 3.7$, $P < 0.001$) larger than the 20 largest females, 315 ± 19.5 (300–367). The largest female, however, was larger than 18 of the largest males.

Number Known Dead—We observed that 12 *C. serpentina* died during the study. A male and a female drowned when the hoop trap they were in collapsed. A male and two females died when struck by vehicles. We do not know the causes of death of the five remaining males and two females. We followed these individuals over several years and captured them numerous times, usually by hand because they would lie in shallow mud near the shore. We found two floating and unable to maintain subsurface activity. We noted each to be emaciated and lethargic. We captured one female initially on 12 March 2010, and recaptured this turtle seven times. On 7 December 2010 she was lethargic and infested heavily with leeches. She died while being measured and weighed on 14 March 2011. More than 300 leeches were removed from below her lower jaw and neck. She had been exsanguinated, and her blood had only a hint of pink color and did not clot. Some of these turtles eat large amounts of elephant-ear (*Colocassia esculenta),* which contains needle-like raphides of oxalic acid monohydrate in its acidic sap. These crystals are known to settle in renal tissues of turtles (Stacey et al. 2008; Jacobson et al. 2009).

Parameter Estimates—Annual apparent survival estimates by sex and age group (Table 2) indicate survivorship was slightly higher for males than for females, though not significantly. Juveniles, however, had a lower estimated survivorship than adult males and females. Estimated population size by age-sex indicates the population may be slightly female-biased, though evidence for this is weak, with juveniles representing about 8% of the total population (Table 2). Probability of capture was not time or group dependent. The annual estimated probability of capture for all individuals was 0.33 (*SE* = 0.02, 95% confidence interval = 0.30–0.36). The estimated population size of males was 90, that of females was 106, and that of juveniles, 18. The estimate for all groups was 215, yielding a density of 26/ha.

Discussion—Flaherty et al. (2008) reported an annual estimated survivorship of 0.97 for adult *C. serpentina*, and noted that the estimate was similar to those reported by Galbraith and Brooks (1987), Congdon et al. (1994) and Galbraith (1994). Our estimates of 0.93–0.94 for adults do not deviate significantly from the results obtained for other unharvested populations. Females at Spring Lake

TABLE 2—Estimated annual population size and survivorship with standard error (*SE*) and 95% confidence intervals (CI) for sex-age groups of *Chelydra serpentina* at Spring Lake, Aquarena Center, San Marcos, Texas.

	Population size			Survivorship		
Age-sex	Estimate	*SE*	95% CI	Estimate	*SE*	95% CI
Males	90.30	4.49	83.98–102.34	0.94	0.01	0.91–0.96
Females	106.68	5.31	98.94–120.43	0.93	0.01	0.90–0.95
Juveniles	18.14	3.24	14.65–28.98	0.81	0.06	0.66–0.90

usually dig their nest chambers within 5 m of the water. Occasional females killed by vehicles do not affect the tertiary sex ratio.

Densities of *C. serpentina* are variable (1–70/ha), and factors affecting densities are not well understood (see Galbraith and Brooks, 1987, for a review). Major (1975), Frose and Burghardt (1975), and Galbraith et al. (1988) reported high densities (59–62/ha). Pearse (1923), Lagler (1943), Hammer (1969), and Galbraith and Brooks (1987) reported low densities (0.17–5/ha). Flaherty et al. (2008) reported a maximum estimated density of 24/ha but noted that the population size increased (96%) during their study. We report a density of 26/ha, which is 41% less than that reported by Major (1975), but similar to that reported by Flaherty (2008). The small habitats where Major (1975) and Frose and Burghardt (1975) conducted their studies may have contributed to the high reported densities. In addition, no other species of turtles was mentioned in either study. Spring Lake and the associated slough were in place 147 y before our study was begun. In addition, *C. serpentina* is the least common turtle at Spring Lake, and accounts for only 4% of the total number of marked turtles (four primary species) inhabiting the system.

Johnston et al. (2012) studied *C. serpentina* for 5 y in the Santa Fe River in northern Florida. They reported that 96% of 113 turtles were captured in a 9-km section of river, providing a density of 2.7/ha.

Reported tertiary sex ratios of *C. serpentina* are usually 1:1 (Frose and Burghardt, 1975; Hogg, 1975; Major, 1975; Galbraith and Brooks, 1987; Flaherty et al., 2008; this study). Galbraith and Brooks (1987) reported on two populations in Ontario, one of which was 300 km north of the other. The southern population was significantly male-biased (1.9:1) and exhibited no sexual dimorphism in adult size. The northern population exhibited no bias in sex ratios, but males were approximately twice the size of females. Johnston et al. (2012) reported an equal sex ratio of *C. serpentina* in the Santa Fe River. Snapping turtles in this population are exceptionally large, which is inconsistent with previous studies (Iverson et al. 1997; Moll and Iverson, 2008) of body size being positively correlated with latitude. The authors presented three factors that may contribute to the large body size: thermal and food resources provided by the artesian springs, the physical environment of the riverine habitat, and coexistence with alligator snapping turtles. Of the three factors, only the presence of alligator snapping turtles is not met at Spring Lake.

Several authors have addressed the issue of unbalanced sex ratios that could be attributed to collection method (Ream and Ream, 1966; Gibbons, 1970; Swannack and Rose, 2003). Data that include a disproportionate number of nesting females would be suspect in establishing population sex ratios. In addition, sex ratios might vary ontogenetically in a population (Swannack and Rose, 2003).

Single-door commercial traps (Frose and Burghardt, 1975; Flaherty et al. 2008) may affect trap success of small and large *C. serpentina* because small individuals generally do not enter traps and larger individuals may be physically restricted from entering. The traps, however, mute the effect of multiple males entering the trap because of the presence of a sexually active female. Larger hoop-traps allow multiple males to enter and although such entry might alter an estimate of capturability of males, the sex ratio should not be affected if the study is of sufficient duration and capture methods are diverse.

Spring Lake is an atypical system where urbanization and habitat modification have not negatively impacted turtle populations, and where the construction of a dam greatly enhanced habitat characteristics favoring high densities and diversity. Nesting aquatic turtles are exposed to various negative impacts induced by urbanization. These include vehicular traffic, terrestrial habitat modification, and low nest and hatchling success caused by increased mesopredators, but the maintenance of a diverse aquatic habitat, part of which has a stable annual temperature, provides ample habitat quality for large numbers of turtles. The presence of four U.S. Fish and Wildlife Service-listed threatened or endangered species (one fish, two salamanders, and Texas wild-rice [*Zizania texana*]) provide a level of habitat protection that otherwise would not be available.

We thank P. Aguirre, T. R. Simpson, F. Weckerly, and J. Tomasso for help or discussion. A. Villamizar translated the abstract. We have complied with all ethical capture and handling procedures to insure protection of the turtles and had a series of Institutional Animal Care and Use Committee approvals over the course of the study.

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Submitted 8 November 2012.
Acceptance recommended by Associate Editor, Neil B. Ford, 28 July 2013.