# POPULATION ECOLOGY OF THE SNAPPING TURTLE (CHELYDRA SERPENTINA OSCEOLA) IN A NORTHERN FLORIDA RIVER

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## **ABSTRACT**

Snapping turtles (*Chelydra serpentina*) occur in nearly every type of freshwater habitat in North America east of the Rocky Mountains, but little is known about the ecology of populations in the southern part of their range, as well as those in lotic habitats. We conducted a mark-recapture study of the Florida snapping turtle (C. s. osceola) in the Santa Fe River in northern Florida between August 2005 and November 2010. Ninety-six percent of all captures occurred within a 9 km section of the river that receives direct input from 21 artesian springs. Within this "high density spring area," population density and biomass of adults were 2.7 turtles/ha and 24.9 kg/ha, respectively. The total sample (n = 113 turtles) consisted of 14.2% immature individuals, 45.1% adult females, and 40.7% adult males. Adult sex ratio was 1:1. Juveniles occupied spring and spring run habitats disproportionally to the river habitat. Adult males (straight midline carapace length [CL] 243–439 mm, mean = 360 mm) are the largest known in Florida, and adult females (CL 257–380 mm, mean = 325 mm) are similar in size to the largest known conspecifics in Nebraska and South Dakota. The large body sizes in our population are inconsistent with previous studies that indicate a positive relationship between body size and latitude in this species, emphasizing the importance of habitat type in influencing demography. Large body sizes in the Santa Fe River may be related to the thermal/food resources provided by artesian springs, the physical environment of the riverine habitat, or coexistence with alligator snapping turtles (Macrochelys temminckii).

**Key Words:** artesian spring, *Chelydra serpentina*, demography, Florida, population, Santa Fe River.

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#### INTRODUCTION

Snapping turtles (Chelydra serpentina) have one of the broadest geographic distributions of all North American freshwater turtles, occurring in nearly every type of lentic and lotic habitat east of the Rocky Mountains (Buhlmann et al. 2008; Ernst & Lovich 2009). Despite many ecological studies of C. serpentina (Stevermark et al. 2008), little is known about populations in the southern part of its range (Aresco & Gunzberger 2007). Less is known about C. serpentina populations in lotic habitats, even though this species is well suited for life in rivers. The characteristics of *C. serpentina* fit many of those described for river-adapted turtles (Moll & Moll 2000), including strong swimmers or bottomwalkers, large size, Type 1 reproduction with many small eggs, diverse foraging abilities, streamlined body shape, and body more dense than water. This gap in the lotic habitat literature is substantial, given the fact that demographic and life history parameters vary widely among populations of C. serpentina and other turtle species (Tinkle 1961; Gibbons & Tinkle 1969; Galbraith et al. 1989; Brown et al. 1994; Iverson et al. 1997; Litzgus & Mousseau 2004; Moll & Iverson 2008; Iverson & Smith 2010). Furthermore, C. serpentina has been harvested historically for food (Clark & Southall 1920; Tucker & Lamer 2004; Aresco et al. 2006), and effective management and conservation of this species requires geographically relevant information.

We conducted a mark-recapture study of *Chelydra serpentina* as part of a broad investigation of the turtle assemblages inhabiting the Santa Fe River in northern Florida (Johnston et al. 2011). Because of the uniqueness of the Santa Fe River population of *C. serpentina* in the southern part of this species' range, we gathered as much information as possible about these turtles. In this paper, we describe spatial distribution, population structure, density, and biomass of *C. serpentina* in the Santa Fe River.

## **MATERIALS AND METHODS**

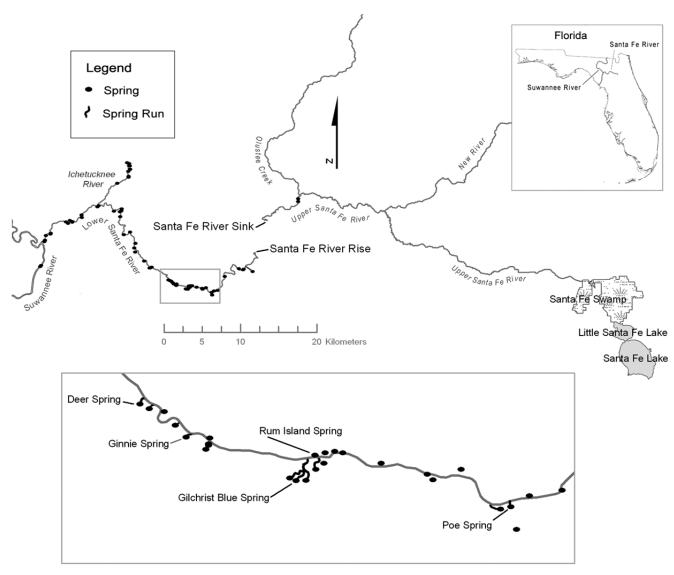
STUDY SITE

Originating in the Santa Fe Swamp in

northern Florida, the Santa Fe River is classified as a blackwater stream due to areas of highly tanninstained water (Florida Natural Areas Inventory 2010), but it is a heterogeneous system that becomes increasingly influenced by springs and, as a result, has enhanced water clarity as it flows along its ~115 km course to the Suwannee River (Fig. 1; Hornsby & Ceryak 1998; Scott et al. 2004; Butt et al. 2007). Approximately 60 km downstream from its origin, the upper Santa Fe River disappears underground into a swallet known as the Santa Fe River Sink (Fig. 1). The subterranean river then re-emerges 5 km away at a site known as the Santa Fe River Rise (Fig. 1). From River Rise, the lower Santa Fe River flows approximately 50 km to the Suwannee River, receiving substantial spring input in its final 37 km.

In the upper Santa Fe River, tannin-stained water inhibits growth of submerged aquatic macrophytes. Vegetation in this portion of the river is therefore limited to patches of emergent and floating plants such as spatterdock (*Nuphar advena* Aiton), duckweed (*Lemna* sp.), water spangles (*Salvinia minima* Baker), and water hyacinth (*Eichhornia crassipes* Martius). Coarse woody debris (e.g., partially submerged fallen trees and completely submerged logs) is abundant. The substrate consists of patches of limestone cobble and a sand/organic mix. The upper Santa Fe River varies in width (2–40 m) and depth (< 1–3 m) during average base flow. Water temperatures fluctuate seasonally (10–30°C).

The habitat in the first 13 km of the lower Santa Fe River is similar to the upper Santa Fe River, except that it is consistently wider (20–30 m) and more thermally stable (20–26°C). In the next 9 km downstream, between Poe Spring and Deer Spring (i.e., the "high density spring area"; Fig. 1), the habitat changes substantially due to direct input from 21 artesian springs (two first magnitude, ten second magnitude, nine third magnitude; Scott et al. 2004). Because of the improved water clarity associated with spring input, this "high density spring area" supports large patches of submerged aquatic vegetation including tapegrass (Vallisneria Michaux), Indian americana swampweed (Hygrophila polysperma Roxburgh), and hydrilla



**Figure 1.** Map of the Santa Fe River drainage in northern Florida. "High density spring area" inset at bottom.

(Hydrilla verticillata Linnaeus). Scattered patches of water hyacinth (Eichhornia crassipes Martius) are also present. Mid-channel water depth varies between 0.5 and 3.5 m. Although the mid channel substrate is generally hard limestone, a soft sand/organic substrate (≤ 1 m deep) occurs along the edge of the river and in the spring runs feeding the river. Water temperatures in this section of the river vary seasonally between 21 and 24°C, but spring water is consistently 22−23°C. Scott et al. (2004) provided a detailed description of the spring habitats and spring runs that connect springs to the river. In the next 17 km downstream, the habitat is

similar to that of the upstream 9 km river reach but current velocity is proportionately greater and soft sand/organic substrate is rare. In the final 11 km of the river downstream from the confluence with the Ichetucknee River, current velocity increases further, and water depth increases substantially (3–5 m). Aquatic plants, soft sand/organic substrate, and coarse woody debris are rare. The substrate is primarily limestone.

## SAMPLING

Turtles were sampled throughout the Santa Fe River, except in the section upstream from the confluence with the New River (Fig. 1), between August 2005 and November 2010 using hoop traps baited with fresh cut fish. Three different trap sizes were used (76 cm diameter, 2.5 cm mesh; 91 cm diameter, 2.5 cm mesh; 122 cm diameter, 6.4 cm mesh) to facilitate placement of traps in sites of varied water depths. Traps were typically placed immediately upstream of snags, submerged logs, undercut banks, and outer bends of the river, with a minimum of 50 m between traps. During each trap session, 8–20 traps were set during late afternoon and checked the next morning. Each trap set overnight constituted one trap-night (TN). Trap captures were supplemented by opportunistic hand captures.

Each captured turtle was measured for straight midline carapace length (CL), maximum carapace length (CL<sub>max</sub>), plastron length (PL), length of posterior lobe of the plastron (PPL), and precloacal tail length (PCL) to the nearest 1 mm using Haglof aluminum tree calipers and weighed to the nearest 1 g using Pesola® spring scales. To individually mark each turtle, we drilled holes in the marginal scutes and peripheral bones using a standard numbering system (Cagle 1939; Froese & Burghardt 1975; Gibbons 1990a) and inserted Passive Integrated Transponder (PIT) tags into the ventrolateral tail muscle (Trauth et al. 1998). Sex was determined by the ratio of PCL to PPL (female < 0.86, male > 0.86; Mosimann & Bider 1960). Females were palpated for eggs, and size at maturity was based on the size of the smallest gravid female. Males were considered mature when they attained a CL at least 55% of the maximum observed in this population (Mosimann & Bider 1960; White & Murphy 1973; Christiansen & Burken 1979). Immature individuals whose sex could not be determined were considered juveniles. whereas immature individuals whose sex could be determined were considered subadults. To quantify the relative difference in body size (CL) between adult females and adult males, we calculated the sexual dimorphism index (SDI) advocated by Lovich & Gibbons (1992): mean size of larger sex divided by mean size of smaller sex with the result arbitrarily defined as positive (minus one) when females are the larger sex and negative (plus one)

in the converse case.

POPULATION DENSITY AND BIOMASS ESTIMATION

Because the population was not evenly distributed throughout the Santa Fe River, we estimated population density within the 9 km (area = 34.9 ha) "high density spring area" between Poe Spring and Deer Spring where 94.6% of all 2005– 2009 captures occurred. To determine population density in this area during 2010, we thoroughly sampled this section of river and all adjacent springs and spring runs, dividing sampling into two periods (period 1: March–June; period 2: July– November). We used the Lincoln-Petersen model to estimate population size. Although riverine turtle populations generally do not meet the assumption of population closure that is necessary for applying the Lincoln-Petersen estimator, we considered it appropriate for Chelydra serpentina at our study site for three reasons. First, a concurrent radiotelemetry study of 10 adult females and 10 adult males in the "high density spring area" provided no evidence of emigration from this area (E. Suarez unpublished data). Second, no individuals trapped in this area were ever trapped outside of this area. Third, only one individual captured outside this area was ever recaptured inside this area. Population size was estimated separately for adult females and adult males. To determine population density, each population size estimate was divided by the area of the "high density spring area" (34.9 ha). Biomass (kg/ha) for each sex was calculated by multiplying population density by mean body mass.

#### RESULTS

SPATIAL DISTRIBUTION

We captured 113 individual *Chelydra serpentina osceola* (253 total captures), but captures were not evenly distributed throughout the Santa Fe River. No individuals were captured in the upper Santa Fe River (40 trap sessions, 423 TN). In the lower Santa Fe River, capture rates were significantly higher in the "high density spring area" (0.21 captures/TN/session, 59 sessions, 923 TN) than in all other areas combined (0.01 captures/TN/session, 30 sessions, 331 TN; Mann-Whitney Rank Sum Test, U = 192.000, p < 0.001). Within

the "high density spring area," capture rates were significantly higher in river habitat (0.27 captures/TN/session, 40 sessions, 637 TN) than in adjacent spring and spring run habitat (0.10 captures/TN/session, 19 sessions, 286 TN; Mann-Whitney Rank Sum Test, U = 162.500, p < 0.001).

#### BODY SIZE AND POPULATION STRUCTURE

Our sample consisted of 7.1% (n = 8) juveniles, 7.1% (n = 8) subadults, 45.1% (n = 51) adult females, and 40.7% (n = 46) adult males (Fig. 2). Immature individuals averaged 179 mm CL (range 40–254; SD = 57.8), 187 mm  $CL_{max}$ (range 43-265; SD = 60.2), 135 mm PL (range 29-193; SD = 44.1), and 1615 g body mass (range 19-3650; SD = 1137.5). The smallest turtle was a hatchling (CL = 40 mm,  $CL_{max}$  = 43 mm; PL = 29 mm; mass = 19 g) captured 31 October 2009 with a yolk scar and no discernible growth annuli. The adult sex ratio did not differ significantly from 1:1  $(\chi^2 = 0.36, df = 1, p = 0.549)$ . Gravid females (n = 14) captured between 8 March and 28 May (86% captured in April) were 257 to 367 mm CL (mean = 320 mm). Adult males were significantly larger than adult females: mean male CL = 359.8 mm (243-439), mean female CL = 324.7 mm (257-380), Mann-Whitney Rank Sum Test, U = 614.000, p < 0.001; mean male CL<sub>max</sub> = 374.2 mm (256–450), mean female  $CL_{max} = 335.8 \text{ mm}$  (272–390), Mann-Whitney Rank Sum Test, U = 543.500, p < 0.001; mean male PL = 262.7 mm (175-318), mean female PL = 246.3 mm (187–293), Mann-Whitney Rank Sum Test, U = 758.000, p = 0.003; mean male mass = 11.46 kg (3.20-20.00), mean female mass = 7.61kg (3.45–11.75), Mann-Whitney Rank Sum Test, U = 572.500, p < 0.001). The SDI using CL was -0.11.

Population structure differed between river and adjacent spring and spring run habitat (Table 1). In particular, juveniles comprised a significantly higher proportion of the sample in the spring and spring run habitat than in the river habitat. The five smallest turtles (40–148 mm CL) were captured only in spring and spring run habitat. The smallest turtle in river habitat measured 149 mm CL.

#### POPULATION SIZE AND BIOMASS

In the "high density spring area" during 2010, the estimated numbers of adult females and adult males were 55 (95% CI = 41–69) and 39 (95% CI = 24–54), respectively. Densities were 1.6 adult females/ha and 1.1 adult males/ha. Because adult females averaged 7.6 kg, adult female biomass was estimated to be 12.2 kg/ha. Adult males averaged 11.5 kg resulting in an adult male biomass estimate of 12.7 kg/ha. When data for both sexes were combined, population density and biomass estimates were 2.7 adults/ha and 24.9 kg/ha, respectively.

## **DISCUSSION**

# SPATIAL DISTRIBUTION

Prior to this study, *Chelydra serpentina* was known to occur in the Santa Fe River, but little was known about population distribution and structure (Iverson & Etchberger 1989; Aresco et al. 2006). This study demonstrates that the population of *C. serpentina* was not evenly distributed throughout the Santa Fe River. The vast majority of individuals occupied a 9 km reach of the lower Santa Fe River and adjacent springs between Poe Spring and Deer Spring. The restricted distribution of this

**Table 1.** Relative proportions of four size/sex classes of *Chelydra serpentina osceola* in two different habitats in the Santa Fe River drainage. Numbers of individuals in parentheses. Of the 113 individuals captured in this study, 16 were captured at least one time in each habitat.

	River	Spring/Spring Run	z-test
Juvenile	0.031(3)	0.147 (5)	Z = 1.999; $p = 0.046$
Subadult	0.053 (5)	0.088(3)	Z = 0.311; $p = 0.756$
Adult female	0.474 (45)	0.382 (13)	Z = 0.725; $p = 0.469$
Adult male	0.442 (42)	0.382 (13)	Z = 0.405; $p = 0.685$

population is not surprising because the springs and spring runs associated with this river influenced the environment in such a way that provided habitat (soft substrate, abundant aquatic vegetation) that C. serpentina is known to prefer (Aresco et al. 2006; Ernst & Lovich 2009). Specifically, greater water clarity enhanced the abundance of aquatic vegetation, and decomposing vegetation helped to create a soft organic substrate. The importance of springs to C. serpentina appears more complex, however. Farther downstream, more springs occurred, but abundance of C. serpentina was relatively low. The low abundance of C. serpentina may be related to less preferred habitat factors such as greater current velocity, greater depths, scarcity of woody debris, or rarity of spring run habitat.

#### POPULATION STRUCTURE

Although adult and subadult Chelydra serpentina used both the river habitat and the adjacent spring and spring run habitat, juveniles less than 149 mm CL appeared to prefer the spring and spring run habitat. This observation parallels the ontogenetic shift in habitat use by C. serpentina in a Michigan marsh (Congdon et al. 1992). In these two very different locations, juvenile C. serpentina appear to behave in similar ways, limiting their activity to shallow and vegetated waters that presumably provide greater foraging success and greater protection from predators. Springs may provide the additional benefit of stable temperatures that maximize growth. If, as suggested by our observations, females in the Santa Fe River nest near springs and, after hatching, juveniles migrate to these springs and spring runs where they spend their first years of life, then these unique habitats could be considered nurseries for *C. serpentina*.

The low number of small turtles in our study does not necessarily indicate low recruitment. These individuals may be common but difficult to sample effectively in spring runs where they can hide in heavy vegetation and bury themselves in soft substrate. They may also be naturally rare in this population due to rapid growth rates that reduce the window of time that this life stage is available for sampling. Germano and Rathbun (2008) reported a similar situation in a western

pond turtle (*Actinemys marmorata*) population that had a population structure caused by relatively fast growth rates rather than a rarity of young turtles. Unfortunately, we know little about juvenile growth rates in our study population. Additional support for the idea that small *C. serpentina* are rare comes from our captures of other small secretive turtle species. We hand captured during day and night 80 striped mud turtles (*Kinosternon baurii*), 73 common musk turtles (*Sternotherus odoratus*), and 391 loggerhead musk turtles (*Sternotherus minor*) in the same areas we found *C. serpentina*, suggesting small *C. serpentina* were not severely under-sampled (Mitchell & Johnston 2012).

The sex ratio between adults in the Santa Fe River population did not differ from 1:1. This is consistent with sex ratios reported from other Florida populations (Aresco et al. 2006; Aresco & Gunzburger 2007; Johnston et al. 2008). Most populations with sex ratios that deviate from 1:1 are in the northern part of the species' range, and they are all male-biased (Kiviat 1980; Galbraith et al. 1988; Steen & Gibbs 2004; Tucker & Lamer 2004; Browne & Hecnar 2007; Iverson & Smith 2010). In northern populations, skewed sex ratios may have been caused by factors such as sampling bias, differences in age at maturity, differential mortality, or nest temperatures that produce mostly males (Gibbons 1990b; Iverson & Smith 2010).

Adults in the Santa Fe River population exhibit a degree of sexual size dimorphism (SDI = -0.11) similar to other reported populations (-0.13 in a Quebec lake, Mosimann & Bider 1960; -0.05 in a South Dakota marsh, Hammer 1969; -0.15 in a Tennessee pond, Froese & Burghardt 1975; -0.03 in a variety of Iowa habitats, Christiansen & Burken 1979; -0.14 and -0.33 in central New York wetlands, Steen & Gibbs 2004; -0.11 in Florida panhandle ponds and a lake, Aresco & Gunzburger 2007; and -0.07 in southern Florida canals, Johnston et al. 2008). However, absolute sizes of females and males are unusually large in the Santa Fe River. In particular, females in the Santa Fe River are larger than any other reported females in Florida (Fig. 2; Bancroft et al. 1983; Aresco et al. 2006; Aresco & Gunzberger 2007; Johnston et al.

2008), and they are equivalent to the largest known females of the species which occur in sandhill lakes in Nebraska (mean CL = 325 mm, size at maturity = 285 mm) and South Dakota (mean CL = 319 mm; size at maturity = 254 mm) (Hammer 1969; Iverson et al. 1997; Moll & Iverson 2008). Fewer comparative data are available for males, but Santa Fe River males are the largest reported in Florida (Fig. 2; Aresco et al. 2006). Large males have been reported from northern populations (429) mm CL<sub>max</sub> in North Carolina [Palmer & Braswell 1995], 415 mm CL in Virginia [Mitchell 1994], 432 mm CL in West Virginia [Green & Pauley 1987], 495 mm CL in Minnesota [Harding 1997], 507 mm CL in Massachusetts [Hunter et al. 1992]), but it is unknown whether these were exceptional individuals or representative of males from their populations. To clarify the apparent uniqueness of Santa Fe River Chelydra serpentina adult body sizes, more data are needed regarding male sizes from populations throughout the species' range, as well as data regarding sizes of both sexes throughout Florida.

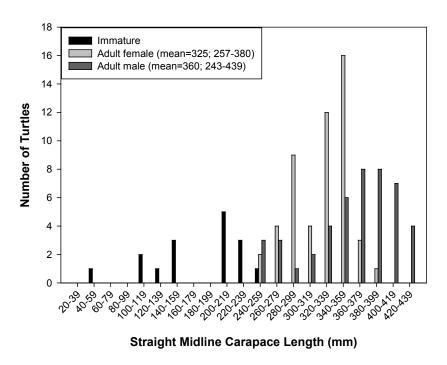
The large body sizes we observed were not anticipated prior to this study. Based on data from populations in lentic habitats throughout eastern North America, Iverson et al. (1997) and Moll and Iverson (2008) reported that average female body size (CL, PL, mass) is positively correlated with latitude and elevation. Our data do not fit that pattern and therefore require explanation. Because published hypotheses explaining large body sizes in populations at high latitudes and high elevations generally involve some aspect of winter survival (Moll & Iverson 2008), we must consider other hypotheses for large body sizes in our northern Florida river where winter temperatures are milder than those typical of northern climates or high elevations. We suspect that some aspect of the habitat is responsible for our observations. Furthermore, the factor(s) responsible for the large sizes of Santa Fe River Chelvdra serpentina probably affect both sexes equally because relative sizes of males and females in this population are similar to relative sizes in other populations.

Perhaps large body sizes are a phenotypic

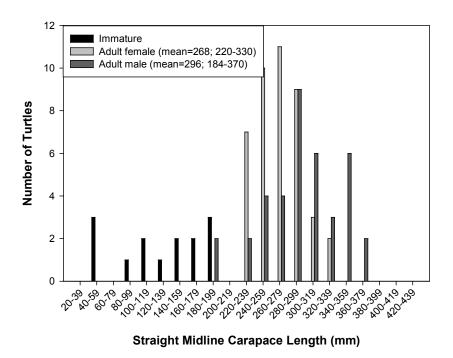
response to habitat that provides conditions for growth. Food abundance, food quality, and temperature are the primary proximate environmental factors affecting turtle growth rates (Gibbons 1967; Moll 1976; Parmenter 1980; Williamson et al. 1989; Avery et al. 1993). Springs may provide the stable water temperatures (i.e., more growing days) and abundant, high quality food sources that maximize growth and body size of Chelydra serpentina. Similar effects have been observed in female vellow-bellied sliders (Trachemys scripta scripta) inhabiting South Carolina's barrier islands (Gibbons et al. 1979) and a lake that receives thermal effluent from a nuclear reactor (Gibbons et al. 1981). Brown et al. (1994) studied the effect of habitat productivity on growth and body size of adult female C. serpentina in Ouebec and observed faster growth rates in a eutrophic pond than in an oligotrophic lake (but no difference in body size). Although fast growth does not necessarily result in larger body size, the cooler temperatures in the Quebec habitats compared to our study site may explain why Quebec snapping turtles in the eutrophic habitat did not grow to larger sizes. If the food resources and thermal regime of springs are responsible for the large C. serpentina body sizes we observed, then large body sizes should not be limited to the Santa Fe River. Rather, they should occur in the many spring runs throughout northern and central Florida. Future studies of growth and body size in Florida spring runs should provide the information necessary to test this "optimal growth conditions" hypothesis.

It is also possible that large body size is a genotypic response to some aspect of the Santa Fe River environment. For example, large body size may be an adaptation that facilitates more powerful locomotion by this bottom-walking species in fast current. Such an adaptation would be analogous to the more streamlined, hydrodynamic shell morphology of riverine river cooters (*Pseudemys concinna*) in comparison with conspecific populations in lentic habitats (Rivera 2008). Another adaptive explanation could be that *Chelydra serpentina* need to be large to coexist with alligator snapping turtles (*Macrochelys*)

## A. Santa Fe River (this study)

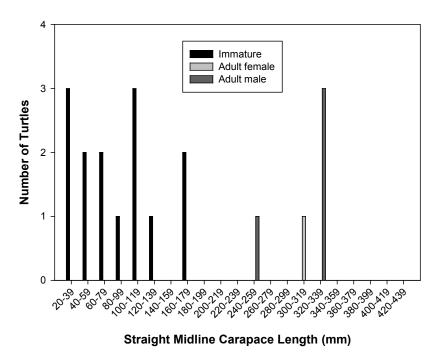


#### B. Florida panhandle ponds and lake (Aresco & Gunzburger 2007)

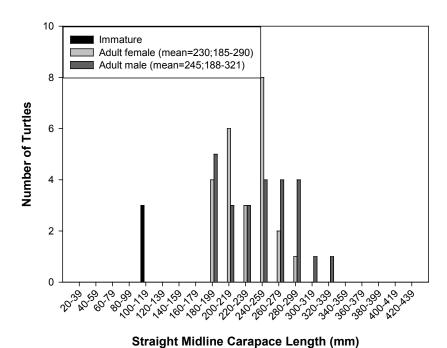


**Figure 2.** Population size structure of snapping turtles (*Chelydra serpentina*) at four different localities in Florida. Each individual turtle is represented once. For turtles captured multiple times, straight midline carapace length (CL) at first capture is used. Midline carapace length is a straight, linear measurement from the anterior edge to the posterior margin at the midline.

# C. Central Florida lake (Lake Conway) (Bancroft et al. 1983)



# D. Broward County canals (Johnston et al. 2008)



temminckii). During this study, we captured 84 M. temminckii throughout the Santa Fe River, including 15 adults (399-623 mm CL, 14.0-54.4 kg) in the "high density spring area" of the lower Santa Fe River, and found both snapping turtle species in the same trap three times. Larger M. temminckii have been reported to attack and kill smaller C. serpentina in captivity, as well as in the wild (Shipman et al. 1994; M. Nickerson in Pritchard 2006). Given the challenges of sharing habitat with M. temminckii, C. serpentina in the Santa Fe River may have adapted to grow larger to survive agonistic encounters with M. temminckii. Large body size in females may also result in increased fecundity to compensate for M. temminckii predation on juvenile C. serpentina. Despite their co-occurrence in the Santa Fe River and many other rivers (Moll & Moll 2004; Buhlmann et al. 2008; Sterrett et al. 2010), surprisingly little is known about the ecological interactions between C. serpentina and M. temminckii.

Throughout North America, larger female Chelydra serpentina produce larger eggs and larger clutch sizes. We have no data on egg size or clutch size for the Santa Fe River population, but the size of the hatchling we captured is consistent with this pattern regarding egg size. This hatchling (CL = 40 mm; no sign of posthatching CL or PL growth) is larger than any other reported wild-hatched hatchling C. serpentina (CL range 16.4–38.1 mm) (Congdon et al. 1999; Ernst & Lovich 2009). Given the strong correlation between hatchling size and egg size (Ewert 1985), this large hatchling probably came from a large egg. Our sample size (n = 1) is obviously small, but this observation suggests that future studies of body size/egg size/ clutch size relationships in this population may be consistent with the currently known pattern and warrants further investigation.

Tropical snapping turtles (*Chelydra acutirostris* and *C. rossignonii*), which may achieve body sizes similar to *C. serpentina* in the Santa Fe River, deviate slightly from the *C. serpentina* body size/egg size/clutch size pattern (Iverson et al. 1997; Moll & Iverson 2008). Specifically, with increasing body size tropical snapping turtles

produce relatively smaller clutch sizes but probably more clutches. It is therefore reasonable to speculate whether *C. serpentina* in the Santa Fe River exhibit a similar pattern. Our limited data suggest they do not. The fact that 86% of the gravid females in our study were captured in April suggests only one clutch is produced per year, which is consistent with all but the southernmost (Miami-Dade County, Florida) *C. serpentina* populations that have been studied (Ewert 2000; Moll & Iverson 2008).

#### POPULATION SIZE AND BIOMASS

Our population density and biomass estimates are difficult to place in context because there are no published data from other lotic habitats with which to compare. In lentic habitats, population density and biomass vary widely from site to site (0.029-67.5 turtles/ha and 0.1-341.3 kg/ha) (Lagler 1943; Hammer 1969; Froese & Burghardt 1975; Major 1975; Kiviat 1980; Petokas 1981; Iverson 1982; Congdon et al. 1986; Galbraith et al. 1988; Congdon & Gibbons 1989; Brown 1992; Iverson et al. 2000; Tucker & Lamer 2004; Dreslik et al. 2005; Stone et al. 2005; Aresco et al. 2006; Reehl et al. 2006; Smith et al. 2006; Johnston et al. 2008; Iverson & Smith 2010). Our data fall within these ranges, but they are comparatively low, especially if all Chelydra serpentina throughout the entire lower Santa Fe River are considered. It is more relevant to consider the possible factors that limit C. serpentina abundance in the Santa Fe River and its adjacent spring systems. Although ten other native turtle species share the river with C. serpentina (Iverson & Etchberger 1989; Meylan 2006; Johnston et al. 2011), competition for food is not a likely limiting factor. Three major components of C. serpentina diet at this site are vegetation, crayfish, and snails, and these prey are all abundant (G. Johnston personal observation). Competition for space may be a factor. Both C. serpentina and Macrochelys temminckii use beaver (Castor canadensis) burrows along the riverbank (E. Suarez, G. Johnston personal observations), and it is possible that agonistic interactions with this larger snapping turtle species limit the availability of this source of shelter. Another form of shelter may be even more limiting, however. In the Santa

Fe River, C. serpentina is not present where soft substrate is rare. All life stages in our population use this substrate for concealment, but it is only available in springs, spring runs, and a relatively narrow (typically  $\leq 5$  m) strip along the river shoreline in the vicinity of springs.

#### ECOLOGICAL STATUS

Our data indicate collectively that there is a small but healthy population of Chelydra serpentina centered in and around the springs and spring runs in the lower Santa Fe River. A key sign of population health is the large body sizes of both sexes. This is especially important given the past history of harvest that occurred in our study area. According to Mark Wray (owner of Ginnie Springs Outdoors since 1971), "turtles of all kinds were hunted by a group of local residents during the 1960s and 1970s to the point they were almost wiped out ... all the turtles we see today, especially the big ones, weren't here 40 years ago." If these anecdotal observations are accurate regarding C. serpentina, then our data describe a population that has recovered from harvest within a relatively short period of time, perhaps because of ideal conditions for growth that may be unique to this habitat. Looking to the future, this population should not experience such a decline again. In July 2009, the Florida Fish and Wildlife Conservation Commission approved a law (Rule 68A-25.002(6)) that prohibited collection of any wild snapping turtles (C. serpentina and Macrochelys temminckii) in the State of Florida. Enforcement of this law (with the help of vigilant local residents, recreational paddlers, divers, and owners of private parks such as Ginnie Springs Outdoors and Gilchrist Blue Springs) will ensure that this unique population of large snapping turtles persists as part of a healthy riverine ecosystem.

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