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Relative Abundance, Population Structure, and Habitat Utilization of the Alligator Snapping Turtle (Macrochelys temminckii) and Eastern Snapping Turtle (Chelydra serpentina) in southeastern Missouri

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Chapter 2

GENERAL ABSTRACT---Alligator Snapping Turtles have not been surveyed extensively in Missouri since 1993-94. Six sites that were sampled in the early nineties were re-sampled in 2009 at the same locations where previous researchers trapped. Significantly fewer significantly fewer Alligator Snapping Turtles were captured per trapnight at all six sites. The population structure of the Alligator Snapping Turtles had a significantly different distribution in 2009 compared to 1993-94. The population structure had shifted toward smaller individuals, and fewer adult males and adult females were captured in 2009 compared to 1993-94. The 1993-94 structure was normally distributed while the 2009 structure exhibited a negative skew. Populations sampled in 2009 have an extremely female-biased sex ratio and fewer large adults, which may impact the population negatively in the future. Future sampling of Alligator Snapping Turtles at these six sites is recommended to continue monitoring their long-term trends in relative abundance and population structure.

Alligator Snapping Turtles (*Macrochelys temminckii*) and Eastern Snapping Turtles (*Chelydra serpentina*) were captured during the summers of 2009 and 2010. Habitat characteristics were collected at each trap that captured these species. Subsequent analysis of data revealed that Alligator Snapping Turtle presence at trap sites was characterized by increased physical structure in the stream, water depth, relatively high levels of detritus, and warmer temperatures when compared to Eastern Snapping Turtles; the amount of aquatic vegetation and bottom surface (i.e., mud or non-mud substrate) were important in characterizing Eastern Snapping Turtle presence in traps.

Eastern Snapping Turtles and Alligator Snapping Turtles did not use the same areas spatially, and were only trapped at the same location once in 557 trapnights. Future conservation plans for the Alligator Snapping Turtle and Eastern Snapping Turtle should consider the microhabitat characteristics of sites utilized by these turtles, along with the possibility of interspecific interactions within Chelydridae.

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CHAPTER 1

CHANGES IN RELATIVE ABUNDANCE AND POPULATION STRUCTURE OF ALLIGATOR SNAPPING TURTLES BETWEEN 1993-94 AND 2009.

Long-lived organisms are difficult subjects for demographic studies because they may outlive the lifespan of a researcher (Reed et al., 2002). As a result of this, long-term studies on these types of organisms are rare in the literature. Although such studies are not frequently undertaken, they are important because the successful conservation of long-lived organisms depends on long-term life history research (Congdon and Dunham, 1997; Congdon et al., 1993; Congdon and Gibbons, 1996; Congdon et al., 1994; Wheeler et al., 2003).

Long-lived animals also possess traits, such as delayed maturation, that impede their ability to respond quickly to increased adult mortality (Congdon et al., 1993; Congdon et al., 1994; Tucker and Sloan, 1997). The delaying of maturation may provide benefits such as higher numbers of offspring, but long-lived organisms like turtles also risk death before reproducing (Congdon et al., 1993). Similarly, populations of long-lived organisms have been shown to be extremely sensitive to even small decreases in adult survivorship of 2% or more because of the delayed time it takes juveniles to reach sexual maturity (Reed et al., 2002). In sea turtles, Spotila and Paladino (2004) showed that adults were the most important size class that needs protection. Contrary to this, in the Missouri hellbender, which can live to 30 years or more, Wheeler et al. (2003) found that lack of recruitment of juveniles was the reason that the population had decreased dramatically between the 1970s and the 1990s. This underscores the importance that the survival of juveniles and eggs can have on population stability. Complementary to these studies, some researchers advocate that protection at all age classes is necessary for assurance of population stability in long-lived organisms (Moll and Moll, 2004; Congdon et al., 1994).

The effects of changes in the survivorship of an age class in long-lived organisms may oftentimes not be evident for years or even decades because of delayed consequences. For example, the results of a decline in births in one year due to increased mortality of adults would not be reflected until that cohort of hatchlings reaches maturity; in Alligator Snapping Turtles this may take over 16 years for females (Tucker and Sloan, 1997). Consequently, achieving results from conservation efforts and plans to aid in the recovery of these species may take a long time as well (Congdon et al., 1993). Needless to say, studying and managing such organisms requires not only time, but patience; and short-sighted values, such as immediate economic gain, frequently interfere with long-term conservation goals (Moll and Moll, 2004; Spotila and Padadino, 2004). For example, commercial harvesting of Alligator Snapping Turtles for food or for the pet trade is a form of exploitation that has repeatedly been shown to be unsustainable, sometimes resulting in the decimation of populations (Pritchard, 2006; Reed et al., 2002; Sloan and Lovich, 1995; Moll and Moll, 2004; Ernst and Lovich, 2009).

The Alligator Snapping Turtle (*Macrochelys temminckii*) is an example of a long-lived organism with a delayed maturation. Age at first reproduction may not be achieved until at least 11-13 years of age (Dobie, 1971), and perhaps not until 16-17 years of age (Tucker and Sloan, 1997). Further limitations to population recovery are that females of this species may not reproduce every year (Ernst and Lovich, 2009; Dobie, s1971). Despite the larger body size of the Alligator Snapping Turtle, clutch size is also usually less than that of the Eastern Snapping Turtle (*Chelydra serpentina*) (Pritchard, 2006), which may inhabit the same bodies of water as the Alligator Snapping Turtle (Shipman and Riedle, 1994) and may compete for resources.

While no long-term studies on relative abundances or population structure exist for *Macrochelys* (Reed et al., 2002), populations of the Eastern Snapping Turtle, the closest relative of the Alligator Snapping Turtle, have been shown to decrease by 65% when large-scale adult mortality occurred due to otter predation (Brooks et al., 1991). This population was stable for nearly two decades prior to this decline. The increase in predation was believed to be a result of meso-predator release. Brooks' study demonstrates the susceptibility of snapping turtle populations to adult mortality.

Shipman (1993) documented the movements of an adult female Alligator Snapping Turtle in Kansas, which was captured incidentally by anglers. He trapped 600 trapnights, and captured 1,022 turtles of varying species, but no Alligator Snapping Turtles. The author believed that numbers of Alligator Snapping Turtles had declined in Kansas. Riedle et al. (2005) compared presence/absence data of Alligator Snapping

Turtles in Oklahoma in 1997-2000 to that of 1970. Alligator Snapping Turtles were only trapped in 5 of the 13 counties where they were trapped in 1970, indicating a shrinking of the Oklahoma distribution. While Riedle et al. (2005) demonstrated a shrinking of the distribution of The Alligator Snapping Turtle in Oklahoma, they did not address specific relative abundance differences between 1970 and 1997-2000. A relative abundance comparison of Alligator Snapping Turtles between two periods in time at specific sites remains to be explored.

In 1993 the Missouri Department of Conservation (MDC) conducted a survey of 211 trapnights, which captured 24 Alligator Snapping Turtles at 4 different sites (Santhuff, 1993). MDC continued surveying the population in 1994, trapping for 275 trapnights and capturing 37 new Alligator Snapping Turtles (2 additional recaptured turtles) at two additional trap sites (Shipman and Riedle, 1994). With limited knowledge of the current status of this species in Missouri, it was important to better understand current status of the species for future management decisions.

The objectives of my study were 1) to assess if the relative abundance of Alligator Snapping Turtles at six sites, where Alligator Snapping Turtles had previously been captured in Missouri, had changed since 1993-1994 and 2) to determine if changes in the population structure of Alligator Snapping Turtles in southeast Missouri occurred between 1993-94 and 2009, and what the implications of those changes may mean for the future of these populations. For objective 1, I predicted I would trap more turtles per trapnight at each site in 2009 than were trapped in 1993-94. This increase in catch per unit effort was expected due to the protected status of the Alligator Snapping Turtle in Missouri and newly protected status in Arkansas, which implemented protection in 1993 (most sites in this study are bodies of water shared with Arkansas). For my second objective, I predicted that the population structure would include a greater number of both large adult and small juvenile turtles than it did in 1993-94 due to protected status in Missouri and Arkansas. To meet these objectives I re-trapped the six sites that had been trapped in 1993-94 and caught Alligator Snapping Turtles. By comparing the distributions of the population of Alligator Snapping Turtles in the early nineties to that of 2009, I hope to learn about shifts in the population, possibly as a result of anthropogenic effects, which may impact the conservation of this species.

MATERIALS AND METHODS

Study Sites—Six sites in southeastern Missouri that had previously been surveyed for Alligator Snapping Turtles and had previously captured Alligator Snapping Turtles (Santhuff, 1993; Shipman and Riedle, 1994) were chosen to be resurveyed in the summer of 2009. Two of these sites were in the St. Francis River watershed, three of the sites were in the Black River watershed, and one site was on the Mississippi River watershed (Figure 1).

The locations within the bodies of water sampled in 1993-1994 were recorded by the previous researchers as "township range and section" (square mile grids). These locations were found using a Missouri Department of Conservation Atlas, and marked on the Atlas. Google Earth software was then used to find the global positioning system location of each town county section on the stretch of river sampled so that the traps could be deployed along the same stretch of river.

The land cover of St. Francis River watershed sites is predominately cropland, but portions of this area consist of bottomland hardwoods including bald cypress (Taxodium *distichum*), water tupelo (*Nyssa aquatica*), red maple (*Acer rebrum*), water hickory (*Carya aquatica*), green ash (*Fraxinus pennsylvanica*), willow (*Salix* sp.), pin oak (*Quercus palustris*), overcup oak (*Quercus lyrata*), and willow oak (*Quercus phellos*). This area floods periodically when the streams are high.

A small remnant section of the Mississippi River watershed was also trapped. This particular bayou is lined with old-growth cypress forests and is subject to periodic flooding.

The Black River watershed was sampled at three sites for turtles. This is a large stream system with numerous conservation areas along its route, which have Cherrybark oak (*Quercus pagota*), sweetgum (*Liquidambar styrasiflua*), red maple, and sugarberry (*Celtis laevigata*) as the primary bottomland species. (Unless otherwise cited, the information on vegetation at the study sites is from the Missouri Department of Conservation Online 2010.)

Trapping Protocol—Lagler hoop traps (consisting of 4 fiberglass hoops, 107cm diameter, 213cm long, and 5cm mesh) were used to sample sites in 2009 (Santhuff, 1993; Shipman and Riedle, 1994). These are the same model and size of trap used in

1993-94. Traps were baited with fresh fish, usually exotic Asian carp (primarily *Hypophthalmichthys* sp.), hooked on a shower hook with no point and no barb, and suspended by twine on the furthest hoop from the throat of the trap.

All turtles caught were measured for carapace length, sexed, and marked on the carapace with waterproof fingernail polish to assist in identifying recaptured individuals. Animals were sexed by comparing the precloacal tail length of the animals relative to their body size (males have a larger precloacal tail length than females and juveniles). Carapace length was measured along the midline of the carapace from anterior to posterior end (median carapace length). Additional measurements were taken on Alligator Snapping Turtles (head width, maximum carapace length, carapace width, plastron length, plastron width, weight, precloacal tail length). Recaptured individuals were only counted once for the relative abundance comparison.

Alligator Snapping Turtles were marked with a passive integrated transponder tag (hereafter referred to as PIT tag) subcutaneously on the ventral side anterior of the inner left hind leg of each turtle (Destron Fearing products). These tags were also used to identify recaptured individuals. To avoid stress or injury, very small juveniles (i.e. less than 20cm carapace length) were not PIT-tagged.

Statistical analysis of the Relative Abundance of Alligator Snapping Turtles—To determine differences between capture rates of Alligator Snapping Turtles in 1993-1994 and 2009 surveys, CPUE (catch per unit effort, where one trap set out for one night equals one trapnight) was compared between sample years using a Wilcoxon match-paired signed-ranks test.

Statistical Analysis of the Population Structure of Alligator Snapping Turtles—I also examined population structure (size, sex, age) changes between the 1993-1994 and 2009 surveys. Due to the low number of captures at a number of locations, individuals captured at all sites were combined. Because of the potential error in determining age and sex, carapace length was used as a proxy of age to compare the population structure of the Alligator Snapping Turtles in 1993-1994 and 2009. Using a two-sample Kolmogorov-Smirnof test, measurements of carapace length from all Alligator Snapping Turtles caught at all six sites in 2009 were compared to the measurements of the turtles caught at all six sites during 1993-1994 to see if the values came from the same distribution. I performed the same analysis using mass as the unit of measurement for size instead of carapace length, because this was used by Shipman and Riedle (2008) to compare the sizes of Alligator Snapping Turtles in the Black River, Mississippi River, and St. Francis watersheds in 1993-94. I compared the sizes of Alligator Snapping Turtles between 1993-94 and 2009 within each watershed (St. Francis River, Mississippi River, and Black River watersheds) using Mann Whitney U-tests. Mann Whitney U-tests were also used to compare the median size of adults between the two sampling periods (1993-94 and 2009) and the median size of juveniles between the two sampling periods to see if classification of the age class was consistent. I then used a Kruskal-Wallace test to compare the mass of turtles among the three watersheds captured only in 2009. The

CPUE of adult males at each site were compared using a Wilcoxon signed-ranks test. Wilcoxon signed-ranks were also used to compare adult female CPUE and juvenile CPUE between the sampling periods.

My study was conducted under Wildlife Collector's Permits # 14134 and # 14548 issued by the Missouri Department of Conservation. Research was conducted under IACUC Protocol # 09-05-05.

RESULTS

Relative Abundance—During the summer of 2009, I trapped a total of 40 Alligator Snapping Turtles at six sites with 3 recaptures. During 1993-94 surveys, a total of 60 Alligator Snapping Turtles were trapped with 2 recaptures at the same sites. Fewer Alligator Snapping Turtles were caught per trapnight at all six sites in the 2009 survey than in the 1993-1994 surveys (Z= -2.201, N=6, P=0.028; Figure 2).

Population Structure—There was a significant difference in the size class distributions between Alligator Snapping Turtles caught in southeastern Missouri in 1993-1994 and those caught in 2009 (Two-sample Kolmogorov-Smirnoff test: Z=1.885, N1=41, N2=61, P=0.002; Figure 3). The 1993-1994 distribution was normally distributed (One-sample Kolmogorov-Smirnoff test: Z=0.572, N=61, P=0.899), while the 2009 distributions exhibited a negative skew toward individuals with a smaller carapace length (i.e. it was not normally distributed; One-sample Kolmogorov-Smirnoff test: Z=1.443, N=41, P=0.031). Because Alligator Snapping Turtles generally reach maturity at minimum sizes of 32.7 cm and 37.8 cm for females and males, respectively (Tucker and

Sloan, 1997), my results suggest a decline in recruitment of mature mid-sized turtles. Interestingly, in 2009 there also were a few large males caught in the over 50 cm size class (N=6); fewer turtles of this size class were captured in 1993-1994 (N=1).

When mass was considered instead of carapace length, the size class distribution in 1993-94 also differed significantly from the 2009 size class distribution; the 2009 mass distribution was shifted toward smaller individuals (Two-sample Kolmogorov-Smirnov Test: KS=1.885, N1993-94=57, N2009=38, P=0.002; Figure 4).

The size (kg) of Alligator Snapping Turtles captured in 2009 on the Black River were significantly smaller than the size of turtles captured there in 1993-94 (Mann-Whitney U=58.5, N1=20, N2=13, P=0.008; Figure 5). In contrast, the size of turtles captured on the Mississippi River watershed in 2009 was significantly larger than the size of turtles captured there in 1993-94 (Mann-Whitney U=109, N1=20, N2=7, P=0.031; Figure 5). There was no significant difference in the size of turtles on the St. Francis River between 1993-94 and 2009 (Mann-Whitney U=108.5, N1=17, N2=18, P=0.142; Figure 5).

The medians of the carapace lengths of all Alligator Snapping Turtles caught in 1993-94 and in 2009 were also compared and found to be significantly different; the median carapace length of turtles in 1993-94 (34.2cm) was larger than that of turtles in 2009 (24.9cm) (U=943.5, N1=60, N2=41, P=0.036).

The Alligator Snapping Turtles captured in the Mississippi watershed in 2009 weighed significantly more than the Alligator Snapping Turtles captured in the Black River (KW=3.456, N=20, P=0.002; Figure 6 and Figure 7) and St. Francis River watersheds (KW=-3.132, N=25, P=0.005), but there was no significant difference in mass between turtles captured in the Black River and St. Francis River watersheds in 2009 (KW=0.618, N=31, P=1.0; Figure 6 and Figure 7).

The CPUE of adult Alligator Snapping Turtles in 2009 was significantly lower in 2009 surveys than in 1993-94 surveys (Wilcoxon signed-ranks test, Z= -2.023, N=6, P=0.043; Figure 8). The ratio of male to female Alligator Snapping Turtles became more female biased in 2009; with 1M: 1.2F in 1993-94, and 1M; 3F in 2009. The mean carapace lengths of juvenile turtles trapped in 1993-94 surveys did not significantly differ from those of juveniles trapped in 2009 surveys (two-sample T(25)= -0.498, P=0.623), and the median carapace lengths of adults turtles trapped in 1993-94 and 2009 did not differ significantly (Mann-Whitney U, N1=51, N2=24, P=0.986).

The CPUE of adult male Alligator Snapping Turtles in 2009 surveys was significantly less than in 1993-94 surveys (Wilcoxon signed-ranks test, Z= -2.023, N=6, P=0.043; Figure 9). The CPUE of adult female Alligator Snapping Turtles was significantly less in 2009 surveys than in 1993-94 surveys, as well (Wilcoxon signed-ranks test, Z=-2.032, N=6, P=0.042; Figure 9). However, CPUE of juvenile Alligator Snapping Turtles did not differ significantly between the two sampling periods (Wilcoxon signed-ranks test, Z=-0.134, N=6, P= 0.893).

DISCUSSION

Fifteen years separated the 1993-94 survey from the 2009 survey. During this time, no comprehensive sampling was conducted on the Alligator Snapping Turtle populations in southeastern Missouri, although limited studies had been conducted at one of the six sites prior to this study (MDC pers. comm.). My study found significant changes in the relative abundance and population structure of Alligator Snapping Turtles in southeastern Missouri between two sampling periods (1993-94 and 2009). Fewer Alligator Snapping Turtles were trapped and at a lower CPUE in 2009 than in 1993-94 surveys. The change in population structure showed a marked decrease in the number of large (adult) Alligator Snapping Turtles from 1993-94 to 2009 surveys. This change was accompanied by an increase in the number of small (juvenile) individuals in 2009. However, the total number of turtles caught was less in 2009 than in 1993-1994, even when effort was taken into consideration. Our results indicate that these populations may be in decline, as is evidenced by the lower catch per unit effort at each site. Moreover, the shift in population structure toward smaller non-reproductive individuals may lead to further population declines in the future.

One potential explanation of the shift in population structure may be an increase in the recruitment of Alligator Snapping Turtles, either by higher nest survivorship, or increased survival of juveniles. This would account for the greater juvenile CPUE in 2009 (0.046 juveniles/trapnight) than in 1993-94 (0.02 juveniles/trapnight). However, this does not explain the overall decrease in turtle abundance or the decrease in adult turtles that occurred between the early 1990's and 2009. Additionally, the increase in number of juvenile alligator snapping turtles was not statistically significant. Moreover, the increase in juvenile turtles and decrease in adult turtles also cannot be explained by a sampling bias toward classifying turtles as juveniles because the carapace size of juveniles and carapace size of adults did not differ significantly between 1993-94 and 2009. Thus, the classification of Alligator Snapping Turtles into groups based on size was consistent between the two sampling periods.

It appears the shift toward smaller Alligator Snapping Turtles is driven by the decrease in sizes of Alligator Snapping Turtles in the Black River watershed. This was the only population that declined significantly in size class between 1993-94 and 2009. Because of this decrease in number of large individuals in the Black River watershed, further studies that focus specifically on the streams within this watershed are recommended, and the trends in population structure and abundance of this stream should be monitored annually. Annually surveying the Black River Alligator Snapping Turtle population will help determine if a decline in large individuals is indeed occurring, what the rate of the decline is, and may provide information on the cause of the decline. It is noteworthy that numerous trotlines and limb lines were encountered in every stream sampled within the Black River watershed, and the effects of these passive fishing methods on Alligator Snapping Turtles should be empirically evaluated.

In contrast to the Black River, the Mississippi River watershed exhibited a significant shift toward larger Alligator Snapping Turtles from 1993-94 to 2009. This system should be monitored, as well, to address if and why there is an increase in large adults at this site. The area of the watershed that was sampled is self-contained and completely enclosed and protected within a public Natural Area. It may be that Alligator Snapping Turtles benefit from this protection, as opposed to having only stretches of the stream or one side of the stream protected. While large adult males and females were trapped in the Mississippi, there was a lack of juvenile Alligator Snapping Turtles trapped there. The need to document juvenile Alligator Snapping Turtles in the Mississippi watershed underscores the importance of continuing to monitor this population. If no juvenile Alligator Snapping Turtles are present at the site it may indicate recruitment problems, or that the young may be utilizing more marginalized areas such as small tributaries and coves, rather than the main channels of the watershed where trapping effort was concentrated.

The reduced number of adult Alligator Snapping Turtles is of particular concern to their successful preservation in Missouri streams. The survival of adult Alligator Snapping Turtles is presumed to be quite high in the absence of anthropogenic pressures (Reed et al. 2002, Ernst and Lovich 2009). Using models based on real life history data based on eastern and Alligator Snapping Turtles, Reed et al. (2002) demonstrated that the stability of Alligator Snapping Turtle populations depends on the high survivorship of the adults, and that even lowering survival from 98% to 96%, will result in population decreases of 50% in less than 50 years. Increased juvenile recruitment is frequently not enough to sustain the population stability of turtles in the event of increased adult mortality (Spotila and Padadino 2004), and the loss of reproductive adults in these organisms is not quickly replaced (Brooks et al. 1991). In sea turtles (Chelonia), which have been considered closely related to Alligator Snapping Turtles (Chandler and Janzen 2009), it has been demonstrated that increasing survivorship in the large sub-adult and adult age classes promotes population growth more effectively than increasing juvenile survivorship (Crouse et al. as cited in Burger and Garber 1995). The increased number of juvenile Alligator Snapping Turtle captures in 2009 surveys could not feasibly compensate for the decrease in adults, because the shift in numbers was not equal, as is evidenced by the overall abundance reduction in 2009. Furthermore, juvenile turtles are not reproductively contributing to the population. The effects of fewer reproductive adult Alligator Snapping Turtles may not be visible yet, and as a result, substantially further decreases in abundance may occur in the near or distant future (Brooks et al. 1991).

The six study sites sampled in southeastern Missouri included three watersheds that hold separate populations of Alligator Snapping Turtles. There is likely little to no immigration, emigration or gene flow between these populations because the stream systems are largely segregated and isolated. This makes them increasingly vulnerable to stochastic and anthropogenic effects because natural recolonization by neighboring populations is unlikely (Roman et al. 1999). Thus, small decreases in survivorship of any age class of local populations are even more deserving of attention and management consideration.

The causes of the decline of adult Alligator Snapping Turtles in Missouri streams remain to be explored. Potential threats to this species are overexploitation, habitat conversion and reduction, pollution, changes in water quality, or a past catastrophe such as a flood. Riedle et al. (2008) documented a similar lack of large adult turtles in eastern Oklahoma, relative to that reported by previous surveys. Riedle et al. state that this decline in large individuals may be attributed to historic harvest in the state. Louisiana, which was the last state to allow commercial harvest of Alligator Snapping Turtles (Pritchard 2006), exhibited a similar skew toward smaller individuals in a trapping survey conducted by Boundy and Kennedy (2003). It is the opinion of many researchers (Reed et al. 2002, Ernst and Lovich 2009, Pritchard 2006) that such declines would not take place naturally because, other than humans, there are no known natural predators of large Alligator Snapping Turtles. Thus, human pressures may be the most important cause of the decline in the numbers of adult turtles. In Missouri and throughout most of its range, it is illegal to harvest Alligator Snapping Turtles, but passive fishing techniques, commercial fishing by-catch, commercial turtle trapping, poaching, and incidental take by anglers may impact turtle populations. During my study I witnessed evidence of turtle mortalities (*Graptemys* sp., *Pseudemys concinna*) as a result of by-catch in legal commercial hoop nets fisheries. I also found a dead Alligator Snapping Turtle floating near several limb lines.

Illegal collectors most likely target larger Alligator Snapping Turtles because they yield more meat. Adult male Alligator Snapping Turtles are sometimes over twice as large as adult females, and so they yield a better price, because, historically trappers were paid by the pound (Pritchard 2006). Jensen and Birkhead (2003) reported trapping fewer 45-90 kg Alligator Snapping Turtles in the Flint River system of Georgia compared to what a commercial trapper from the area reportedly caught in the 1970's. Turtles in the 45-90 kg range are probably all males. If indeed illegal collecting is taking place in Missouri, a bias toward large turtles could explain the drastic reduction in male Alligator Snapping Turtles trapped in 2009 compared to 1993-94, and the skewed sex ratio toward females in 2009. Alligator Snapping Turtles exhibit temperature-dependent sex determination (Ligon and Lovern, 2009), which may be a cause of the sex bias toward females. Previous researchers have called for more studies on turtle populations that have extremely biased sex ratios (Marchand and Litvaitis 2004). Long-term investigations into wood turtle populations revealed that a reduction in number of adult females and number of juveniles preceded population declines and subsequent extinctions of populations (Garber and Burger 1995). While the reduction of turtles in that survey occurred in females and juveniles, the study highlights the negative influence that unnaturally skewed sex ratios can exert upon populations.

Given the life history traits of the Alligator Snapping Turtle, such as being long-lived, slow to reach reproductive age, and lacking of terrestrial migratory movements, these animals are less likely to recover quickly from population declines (Brooks et al. 1991) and immediate conservation action may be necessary to maintain or establish stable populations. While I acknowledge that this study is representative of only two sampling periods (early 90's and 2009), and that instability of populations may be overestimated based on studies of short duration (Wheeler et al. 2003), the broad consistency of the results of this study appear to be a strong indication that populations of Alligator Snapping Turtles in southeastern Missouri need to be monitored more closely to determine if declines are indeed occurring, and what the results of the apparent sex bias in the populations may be.

Thus, Missouri's population of Alligator Snapping Turtles at these six sites warrant further trapping and tagging studies to continue monitoring relative abundances and population structure. Incorporating studies addressing the causes of the decline in these populations will insure the future of this rare species in Missouri streams, in which it is an integral part of the maintenance of healthy aquatic systems at the northern edge of its distribution.

Based on the current study, I propose several recommendations aimed at conservation and management efforts for this turtle:

1) When possible, land should continue to be acquired by the State of Missouri in areas where Alligator Snapping Turtles are known to exist. Alligator Snapping Turtles were often more abundant outside of public land boundaries. These areas are not within protected public areas, and protection of the Alligator Snapping Turtle would be enhanced by obtaining land on these stretches of rivers. Many public lands areas exist only on one side of a stream, and in effect, do not protect the animals within the stream from passive fishing techniques that are legal on the other bank (e.g. commercial fish or

turtle trapping or limb lines and trotlines). Establishing public land areas on both sides of the streams is vital to successful conservation of this species. If purchasing these lands is not feasible, eliminating commercial fishing, commercial turtle trapping, trotlines, and limb lines in these areas would benefit the Alligator Snapping Turtle. Establishing conservation easements is another possible avenue that would benefit this species if land cannot be purchased outright.

2) Establishing buffer zones along streams known to have Alligator Snapping Turtles would enhance their conservation. Protected riparian areas of at least 100-m or greater are recommended based on the distance of Alligator Snapping Turtle nests from the water line (Pritchard 2006). Bodie (2001) recommends a 150-m riparian area to protect most turtle species. These estimates still may not be enough, and some researchers have called for 275-m buffer zones to protect 100% of turtle species within a given watershed (Burke and Gibbons 1995). Adequate buffer zones to protect nesting sites of this species may vary geographically, and further studies on buffer zones and nesting sites are needed to establish what the optimal size stream buffers are for Alligator Snapping Turtles in Missouri.

3) Enforcement of existing regulations is recommended. Some of the sites sampled occur within public land areas, where limb lines, trotlines, and commercial trapping are illegal. Yet trotlines and limb lines were visible at all of the sites sampled, including within public land areas. In the words of John Terborgh (as cited in Spotila and Paladino 2004) “There is no substitute for enforcement.” Enforcement of the protected status of

the Alligator Snapping Turtle in these extensive tracts of streams and banks is not easily accomplished, especially with limited person power and resources. Despite these limitations, Missouri Department of Conservation agents do put a great deal of effort in upholding Missouri regulations (in fact, some agents assisted with this study), but additional manpower is badly needed.

4) Restricting commercial fishing and turtle trapping in the areas where Alligator Snapping Turtles were found is also strongly recommended. I encountered commercial fishing hoop nets that were filled with dead false map turtles (*Graptemys psuedogeographica*), river cooters (*Pseudemys concinna*), and red-eared sliders (*Trachemys scripta*) at one public land area. I did catch one Alligator Snapping Turtle in our traps at this site, but given the suitability of the available habitat at the site, it is surprising that more Alligator Snapping Turtles were not caught. Due to the high number of other species of turtles caught in commercial fishing traps, it is likely that these commercial fishing traps result in mortality of Alligator Snapping Turtles.

5) Increasing outreach and education on the importance of turtles in Missouri waters is especially important in the southeast regions of Missouri, in which the Alligator Snapping Turtle is found. As an example, I have already initiated outreach by visiting Missouri schools to discuss the importance of protecting the Alligator Snapping Turtle and their habitat. Perhaps community involvement in assisting conservation agents may instill a sense of stewardship in citizens, who along with the future generations of

Missourians, have the right to enjoy healthy natural stream ecosystems in which large, long-lived turtles still thrive.

In summary, my study found that Alligator Snapping Turtles in southeastern Missouri may be undergoing a decline and changes in their population structure that do not bode well for the future of this species. I urge that additional studies be conducted on this species and that greater conservation and education efforts be undertaken.

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FIGURES

Figure 1. Streams where Alligator Snapping Turtles (*Macrochelys temminckii*) were trapped in Missouri in the summer of 2009.

Figure 2. Differences in Alligator Snapping Turtles (*Macrochelys temminckii*) captured per trapnight between 1993-94 and 2009 surveys at six sites. Capture rate in 2009 was significantly less than in 1993-94 (Z= -2.201, N=6, P=0.028).

Figure 3. Comparison of size class distributions (carapace length measured in cm) of Alligator Snapping Turtles (*Macrochelys temminckii*) between 1993-94 and 2009 surveys. Arrows indicate mean carapace length for 1993-94 (gray arrow) and 2009 (black arrow). M-arrow indicates minimum size of mature males (38 cm), and F-arrow indicates minimum size of mature females (33 cm).

Figure 4. Size (mass measured in kg) of Alligator Snapping Turtles (*Macrochelys temminckii*) captured in 1993-94 and in 2009. The distribution of 1993-94 was significantly different than the 2009 distribution (Kolmogorov Smirnov Test: KS=1.885, N1993-94=57, N2009=38, P=0.002).

Figure 5. Comparison of the means of Alligator Snapping Turtle (*Macrochelys temminckii*) mass between 1993-94 and 2009 at three watersheds. Black rings indicate

the mean mass (kg) at each watershed in 2009. The black triangles indicate the mean mass at each watershed in 1993-94.

Figure 6. Number of Alligator Snapping Turtles (*Macrochelys temminckii*) captured in each size class (mass measured in kg) at the Mississippi River, St. Francis River, and Black River watersheds in 2009.

Figure 7. Boxplot of the mass of Alligator Snapping Turtles (*Macrochelys temminckii*) captured at the St. Francis River, Mississippi River, and Black River watersheds in 2009. The shaded box represents values within the 25th through the 75th percentile. The black line within each box represents the median. The whiskers represent the minimum and maximum values within 1.5 box lengths of the 25th and 75th percentile. The asterisks and open circles represent outliers that are beyond 1.5 box lengths of the 25th and 75th percentiles.

Figure 8. Comparison of the number of adult and juvenile Alligator Snapping Turtles (*Macrochelys temminckii*) captured between 1993-94 and 2009 surveys. The difference between number of adults captured in the two sampling periods was significant even when adjusted for effort (Z=-2.023, N=6, P=0.043). The difference between number of juvenile captured in the two sampling periods was not significant (Z=0.134, N=6, P=0.893).

Figure 9. Comparison between total number of adult male and adult female Alligator Snapping Turtles (*Macrochelys temminckii*) trapped in 1993-94 and 2009 surveys. The

difference between number of males captured in each survey was significant ($z = -2.023$, $n=6$, $p=0.043$), and the difference between number of females captured in the two sampling periods was significant ($Z=-2.032$, $N=6$, $P=0.042$).

Figure 1.

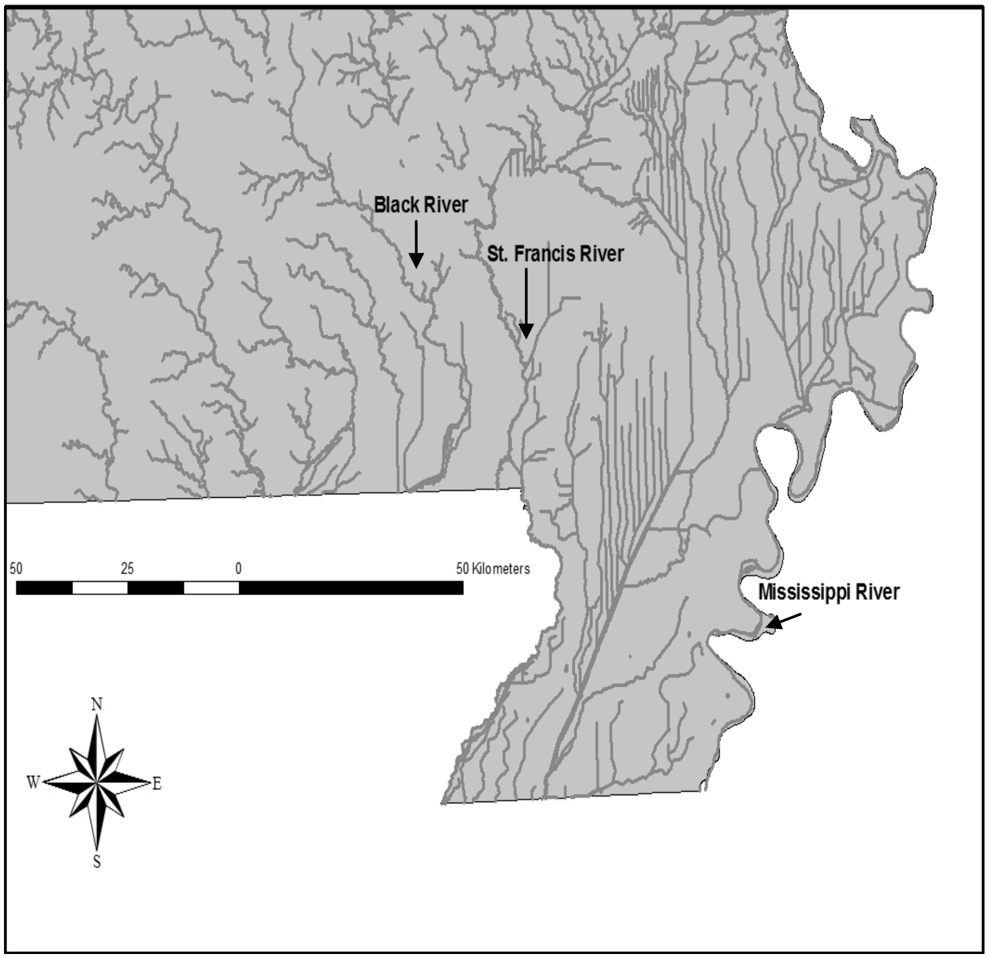

Black River
St. Francis River
Mississippi River
50
25
0
50 Kilometers
N
W
E
S

Figure 2.

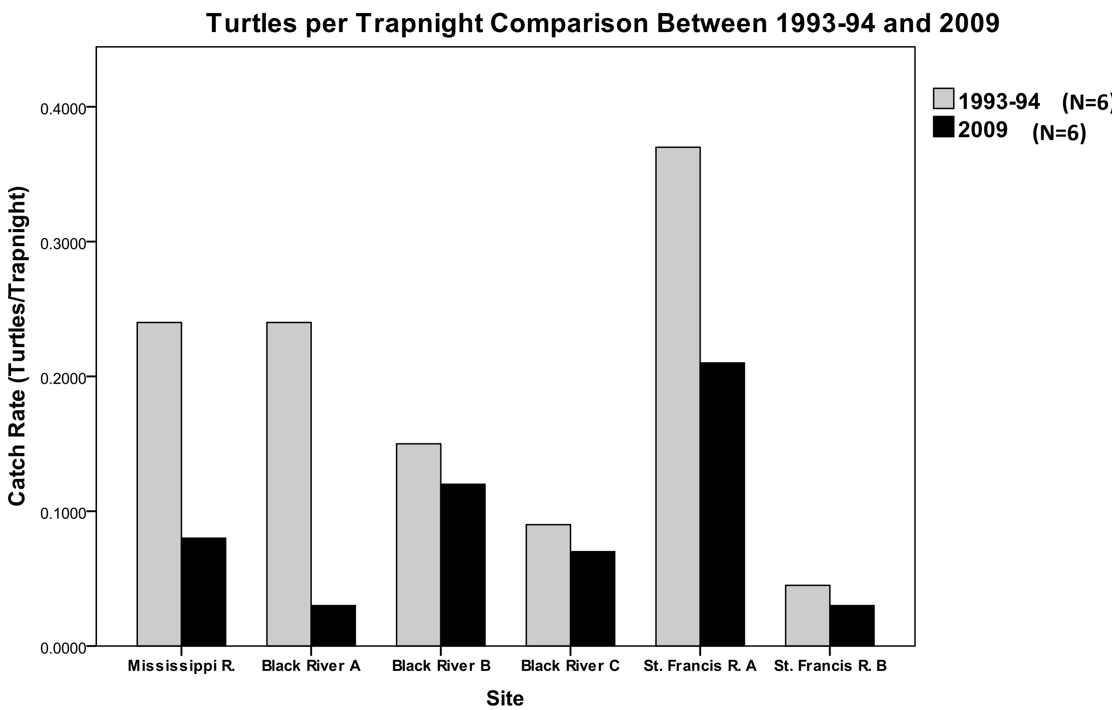

Turtles per Trapnight Comparison Between 1993-94 and 2009
Catch Rate (Turtles/Trapnight)
0.4000
0.3000
0.2000
0.1000
0.0000
Mississippi R.
Black River A
Black River B
Black River C
St. Francis R. A
St. Francis R. B
Site
1993-94 (N=6)
2009 (N=6)

Figure 3.

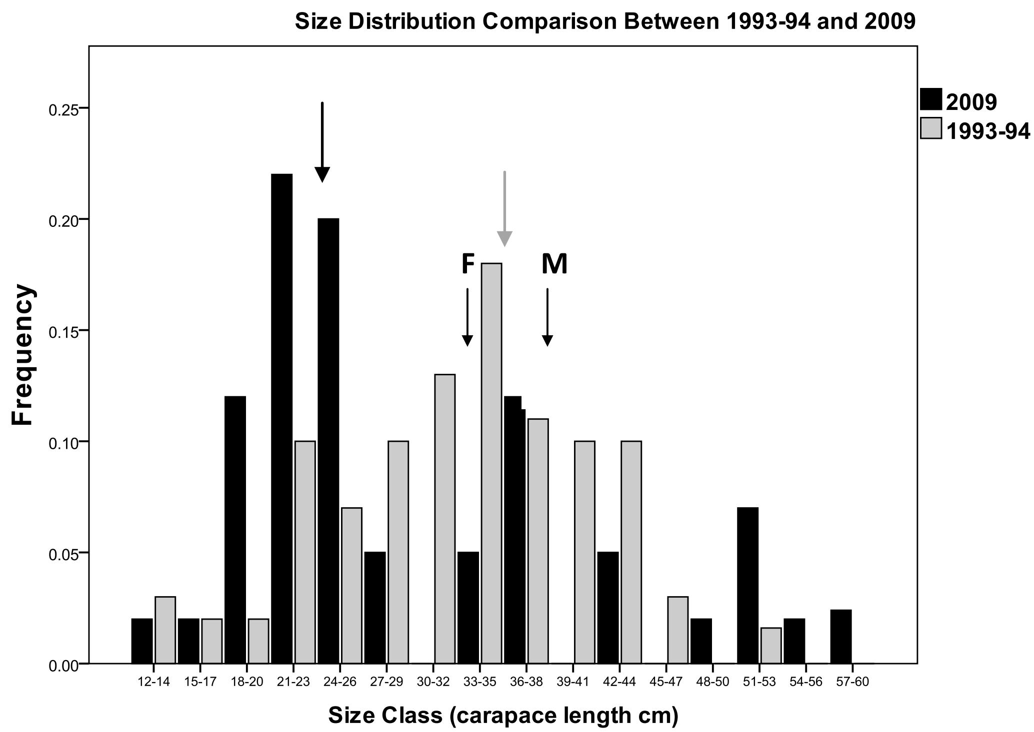

Size Distribution Comparison Between 1993-94 and 2009
2009
1993-94
F
M
Frequency
0.25
0.20
0.15
0.10
0.05
0.00
12-14
15-17
18-20
21-23
24-26
27-29
30-32
33-35
36-38
39-41
42-44
45-47
48-50
51-53
54-56
57-60
Size Class (carapace length cm)

Figure 4.

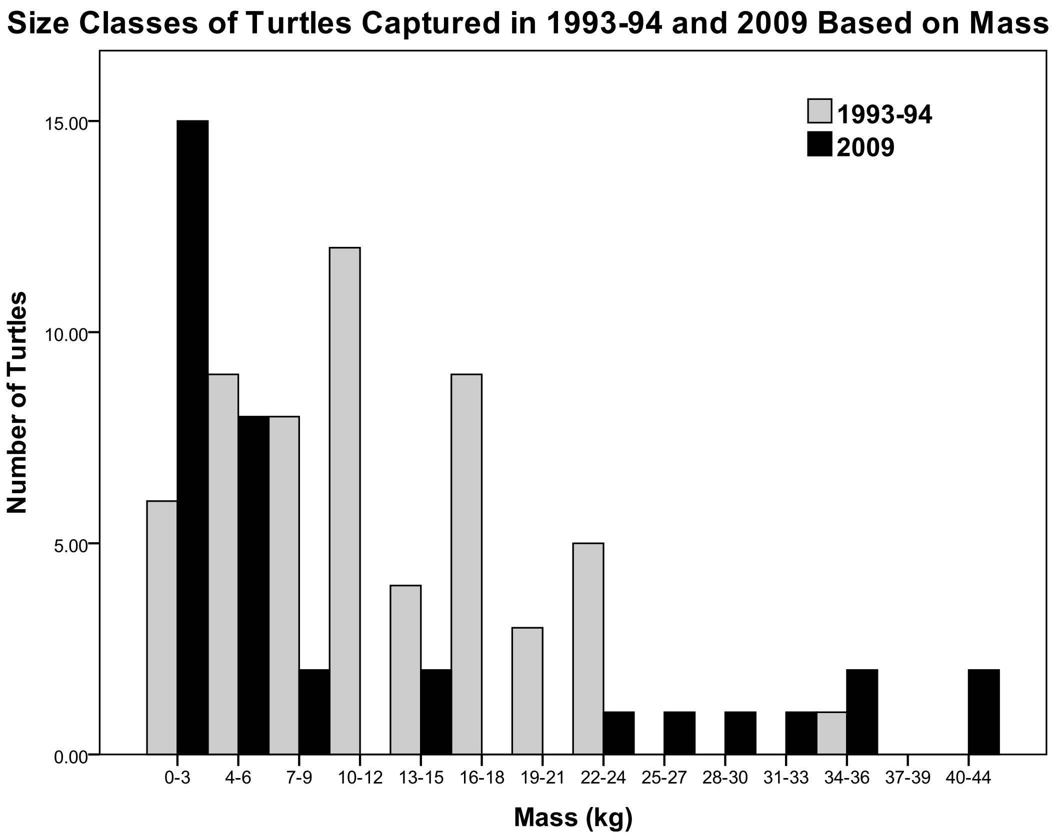

Size Classes of Turtles Captured in 1993-94 and 2009 Based on Mass
1993-94
2009
Number of Turtles
15.00
10.00
5.00
0.00
0-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
28-30
31-33
34-36
37-39
40-44
Mass (kg)

Figure 5.

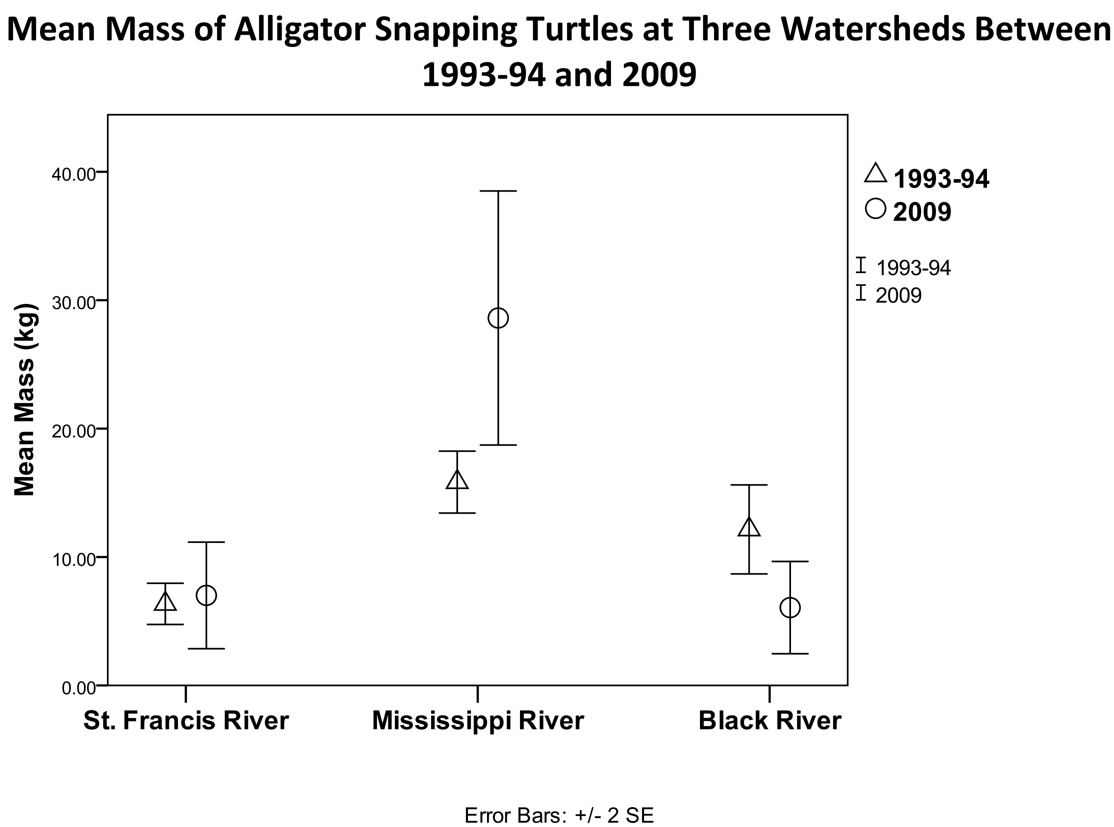

Mean Mass of Alligator Snapping Turtles at Three Watersheds Between 1993-94 and 2009
Mean Mass (kg)
40.00
30.00
20.00
10.00
0.00
St. Francis River
Mississippi River
Black River
1993-94
2009
1993-94
2009
Error Bars: +/- 2 SE

Figure 6.

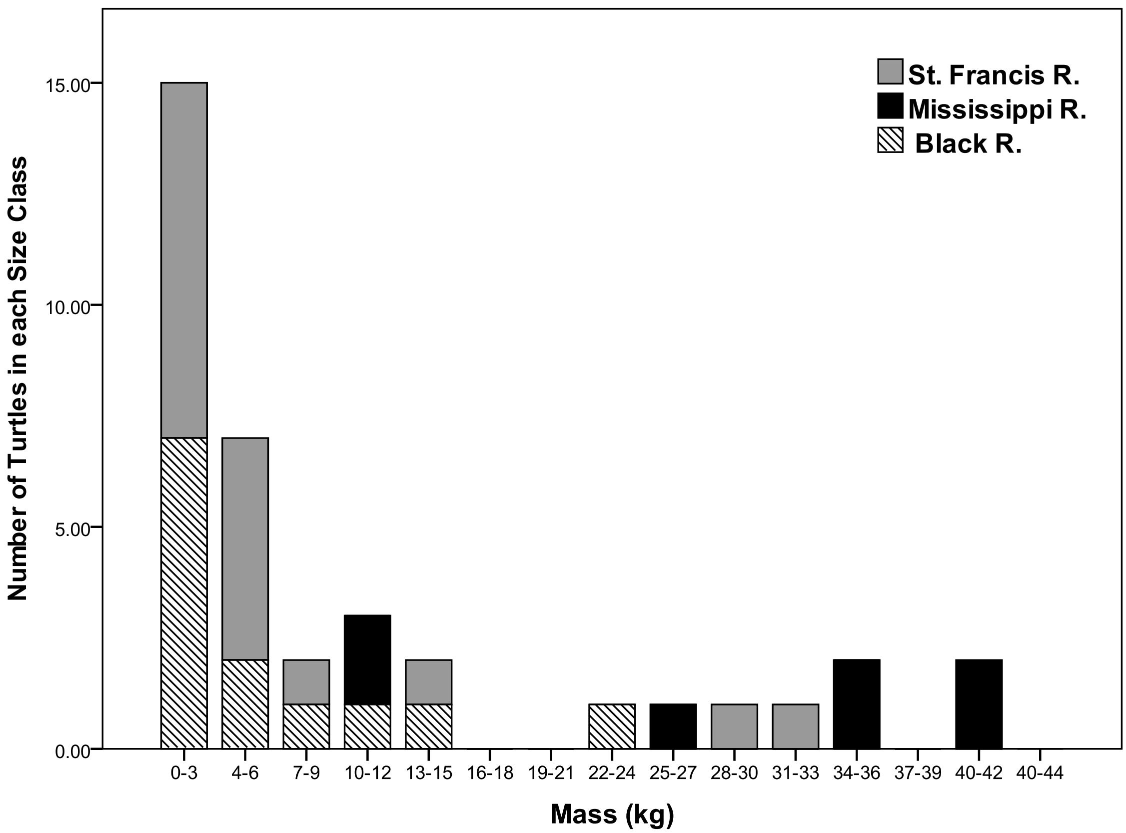

St. Francis R.
Mississippi R.
Black R.
15.00
10.00
5.00
0.00
Number of Turtles in each Size Class
0-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
28-30
31-33
34-36
37-39
40-42
40-44
Mass (kg)

Figure 7.

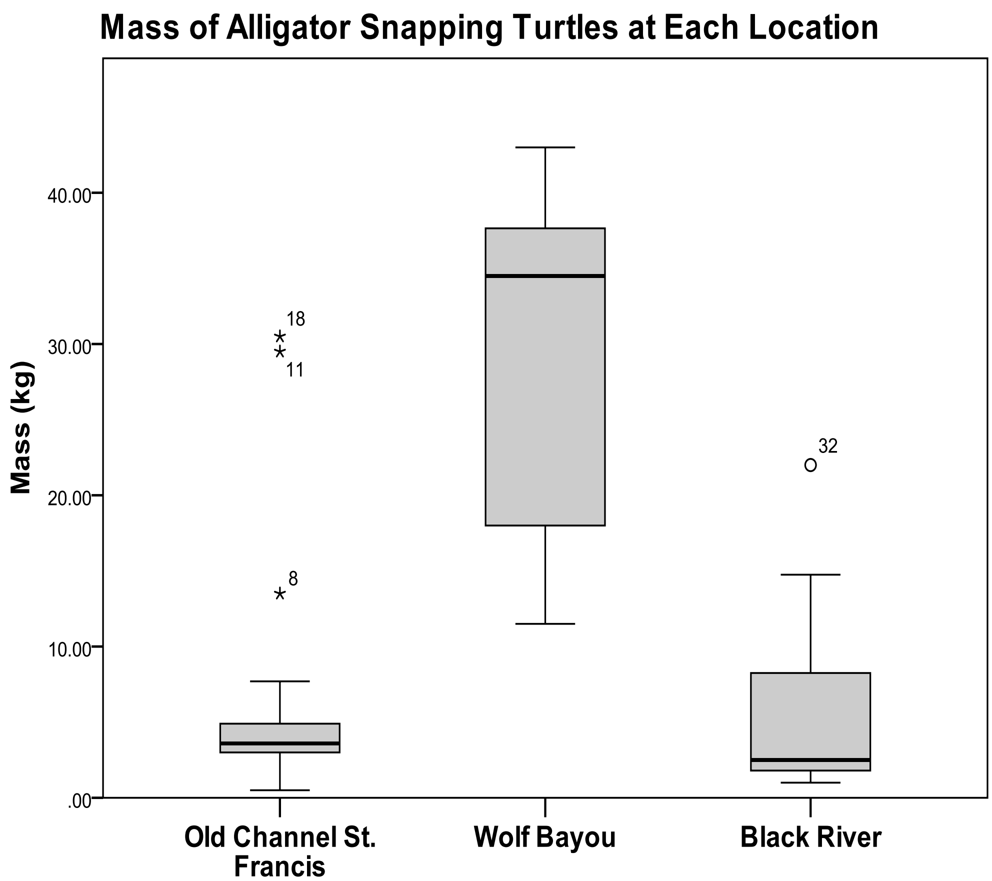
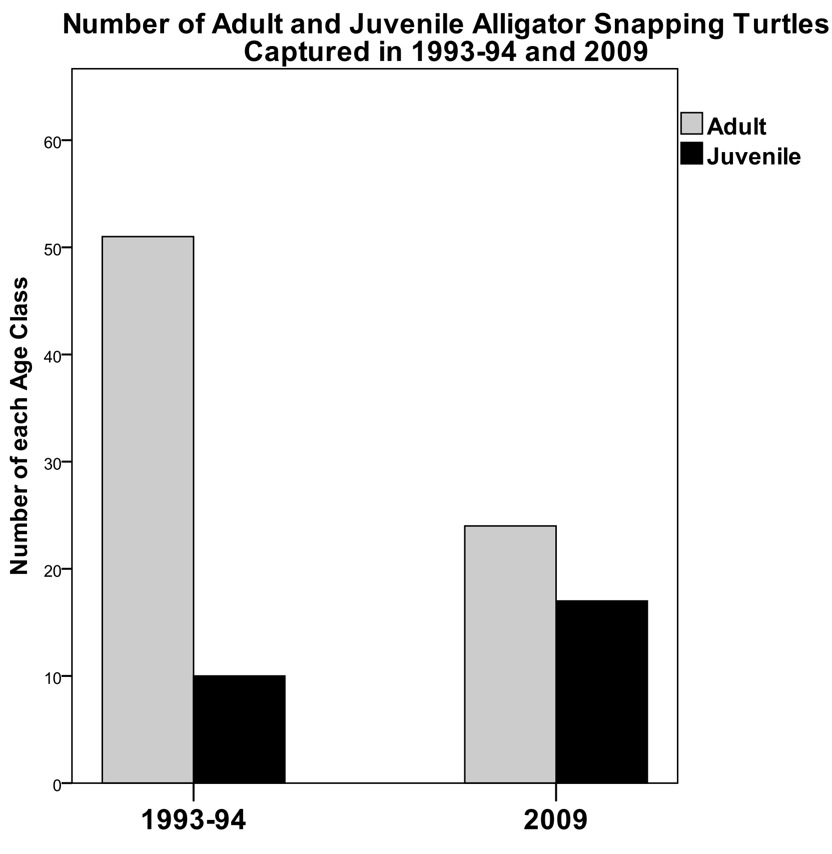
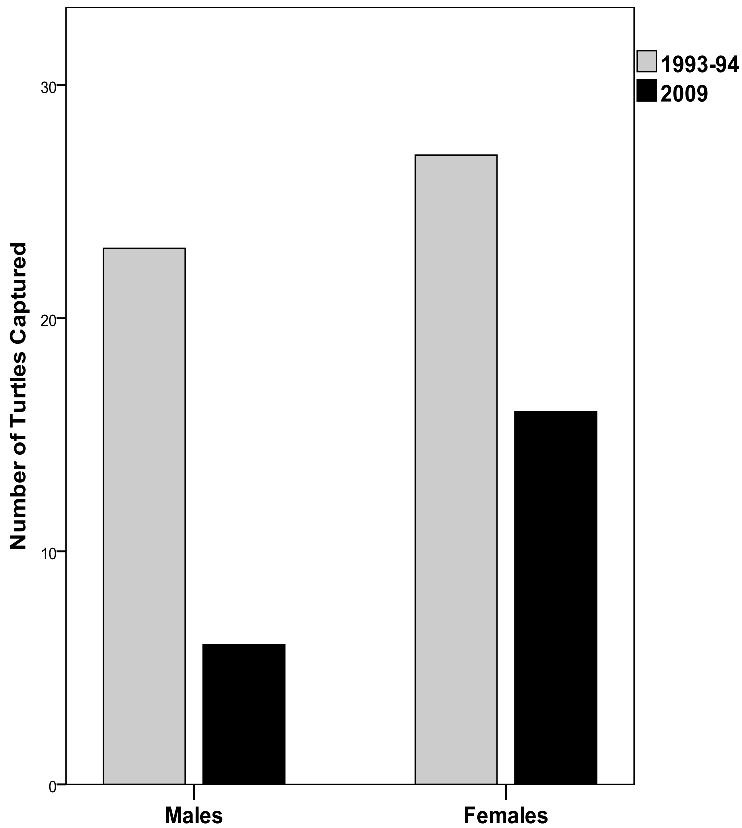

Mass of Alligator Snapping Turtles at Each Location
Mass (kg)
40.00
30.00
20.00
10.00
.00
18
11
8
32
Old Channel St. Francis
Wolf Bayou
Black River

Figure 8.



Number of Adult and Juvenile Alligator Snapping Turtles Captured in 1993-94 and 2009
Adult
Juvenile
Number of each Age Class
0
10
20
30
40
50
60
1993-94
2009

Figure 9.


1993-94
2009
30
20
10
0
Number of Turtles Captured
Males
Females

CHAPTER 2

HABITAT USE BY THE ALLIGATOR SNAPPING TURTLE (*MACROCHELYS TEMMINCKII*) AND EASTERN SNAPPING TURTLE (*CHELYDRA SERPENTINA*) IN SOUTHEASTERN MISSOURI: IMPLICATIONS FOR INTERSPECIFIC COMPETITION

In order to reduce (or possibly as a result of) interspecific competition, resources may be partitioned among species by time, food type, or space (Moll and Moll, 2004). This partitioning is possible because although some species are better adapted to certain environments, others may exhibit a greater range of behavioral plasticity in dealing with environmental constraints or pressures (Simmonds and Isaac, 2007). The plasticity of species can allow them to coexist in or near the habitat of the other species (Vogt, 1981).

Partitioning of habitat resources has been documented in a wide variety of organisms, including turtles (Lindeman, 2000; Moll and Moll, 2004; Luicelli, 2008). For example, the White-lipped Mud Turtle (*Kinosternon leucostomum*) eats less animal matter where it occurs in sympatry with the molluscivore specialist the Giant Mexican Mud Turtle (*Staurotypus triporcatus*). *K. leucostomum* also utilizes shallower pools than *S. triporcatus* in these areas (Vogt and Guzman, 1988). Differential utilization of streams has been observed in the Spiny Softshell Turtle (*Apalone spinifera*) and the Smooth Softshell Turtle (*Apalone mutica*), two closely related congeners that inhabit Missouri rivers and streams. *A. spinifera* occupies closed side channels and tributaries in areas of slow-moving water and high visibility, whereas the *A. mutica* predominates in fast-moving, deep areas near the main channel (Barko and Briggler, 2006). In the Northern Map Turtle (*Graptemys geographica)*, Ouachita Map Turtle (*G. ouachitensis*), and False Map Turtle (*G. pseudogeographica pseudogeographica*), partitioning exists in areas where the species overlap. *G. geographica* utilizes rock and gravel substrates and benthically feeds on mollusks; *G. ouachitensis* is an omnivorous surface feeder, and utilizes mud, sand, and rock; and *G. p. pseudogeographica* is an omnivorous bottom and surface feeder, and utilizes mud substrates (Dunson, 1981; Vogt, 1981).

Partitioning of resources may occur in other species of turtles in Missouri, including the only extant representatives from the family Chelydridae, the Alligator Snapping Turtle (*Macrochelys temminckii*), and the Eastern Snapping Turtle (*Chelydra serpentina*). These two species have been observed in interspecific agonistic interactions (Shipman and Edds, 1994), they are closely related (Chandler and Janzen, 2009), and they may have similar microhabitat habitat requirements (Riedle et al., 2009).

Previous studies that have examined habitat use by the Alligator Snapping Turtle and Eastern Snapping Turtle suggest that the microhabitat each species occupies may vary geographically, seasonally, and as a result of the environmental context (e.g., presence of other species). For example, Alligator Snapping Turtles have been found to use streams with abundant physical structure, high percentage of overhead canopy cover, and low bank gradients (Harrel et al., 1996a; Riedle et al., 2006; Shipman and

Riedle 2008; Howey and Dinkelacker, 2009). Eastern Snapping Turtles tend to use shallow pools with abundant aquatic vegetation, increased physical structure (Froese, 1978; Ernst and Lovich, 2009), and are less abundant in streams with high turbidity (Ernst and Lovich, 2009). In Ontario, Obbard and Brooks (1981) found that Eastern Snapping Turtles utilized lilies for structural cover and food. In Japan, where *C. serpentina* is an introduced species, it spends more time in streams than in adjacent agricultural areas (Kobayashi et al., 2006). Riedle et al. (2009) found that both species of snapping turtles were generalists in Oklahoma and were associated with slower streams and backwater habitats. Moll and Moll (2004) considered the Alligator Snapping Turtle as more of a specialist river turtle, but categorized the Eastern Snapping Turtle as a generalist and not a true river turtle. The microhabitat each species occupies may vary geographically, seasonally, and with environmental parameters, such as the presence of the other species.

While multiple habitat studies have been made on the Alligator Snapping Turtle (Harrel et al., 1996a; Shipman and Riedle 2008; Howey and Dinkelacker, 2009) and Eastern Snapping Turtle (Froese, 1978; Kobayoshi et al., 2006), none of these studies has attempted specifically to compare the habitat characteristics utilized by each species with that of its closest relative in the same study to address the differences in the habitat of the two species. Similarly, the previous studies address the spatial locations of the Alligator Snapping Turtle and the Eastern Snapping Turtle, but not in relation to one another.

The objective of this study was to compare microhabitat characteristics between sites utilized by Alligator Snapping Turtles and sites utilized by Eastern Snapping Turtles. While we did not test competition between these species directly, if habitat partitioning is occurring due to interspecific competition, we would expect the two species to use different types of microhabitat to minimize the negative effects of competition. Our prediction was that, due to its highly specialized aquatic nature, the Alligator Snapping Turtle would inhabit deeper pools, areas with increased amounts of physical structure in the stream, areas of higher percentage of canopy cover, and lower bank gradients (Shipman and Riedle 2008), while the Eastern Snapping Turtle, because it is more of a generalist, would not be restricted to these areas, and would also be trapped in more degraded and poorer quality habitats. We also predicted that Alligator Snapping Turtles would not be trapped in the same areas as the Eastern Snapping Turtle, possibly to minimize interspecific competition. This is the first study that specifically compares the habitat utilization of the Alligator Snapping Turtle and Eastern Snapping Turtle in bodies of water where both species occur.

MATERIALS AND METHODS

Study Site—During the summers of 2009 and 2010, we trapped six watersheds in southeastern Missouri for Alligator Snapping Turtles and Eastern Snapping Turtles. These included the Mississippi River, Castor River, St. Francis River, Black River, Current River, and Eleven Point River (Figure 1). Many of these rivers have been modified (channelized, dammed), but in small sections have been restored to allow natural flooding of wetlands. In the areas trapped on the Castor River, St. Francis River, Black River, and Mississippi River, these streams were lowland meandering warm-water rivers. The Eleven Point River and Current River are cold-water spring-fed streams, typical of the higher elevation of the Ozark Highlands.

Trapping Design—The specific location where each trap was set within the six sites was made using the historical trap locations from the Missouri Department of Conservation (Santhuff 1993, Shipman and Riedle 1994). Township, Range, and Sections were used by previous researchers in 1993-94 to mark their trap locations. We marked these locations on a map using an MDC Atlas, and then over-laid the locations on Google Earth maps to determine the specific GPS locations where the traps had been set in 1993-94. We then returned to these sections of the streams and set the same number of trapnights in each section that the previous researchers had set. At certain sections sites we could not set the same number of traps due to complications such as weather or log jams, so trapping effort was normalized across sites by using the number of turtles caught per trapnight as the catch per unit effort (where ten traps set for one night equals ten trapnights).

The habitat where each species was captured was assumed to be used by these turtles (e.g., for foraging), rather than locations where turtles were simply passing through and inadvertently caught. Alligator Snapping Turtle habitat and Eastern Snapping Turtle habitat at each trap site were evaluated in terms of: distance to nearest shore (measured in cm); water depth (measured with a weighted measuring tape in cm); canopy cover (measured as the amount of light passing through the canopy to the stream with a densiometer); physical structure in the stream (measured by the amount of woody structure in the water column: 0=no structure at surface or underwater, 1=minimal structure either underwater or at surface, 2=many overhanging roots and structure at surface and underwater, 3=log jam); water temperature at surface (measured in degrees Celsius); bank gradient (degree of incline of nearest bank measured with a roofer's angle finder); and number of tributaries within 25m of the location of the turtle (0=no tributaries, 1=one tributary, 2=2 tributaries, 3=3 tributaries); percent detritus, qualified as presence of leafs, sticks, and organic debris above substrate, within 3 m of the trap (measured by taking 10 samples by hand, 5 samples on both sides of the trap; this was converted into a percentage of handfuls that had detritus); type of substrate (mud present or no mud); presence or absence of aquatic vegetation (0=absence of aquatic vegetation, 1=presence of aquatic vegetation); stream classification (1=pool, 2=run, 3=riffle). In 2010, the following additional habitat characteristics were measured: dissolved oxygen (measured with a DO meter at the throat of each trap); turbidity (measured with a sechi disc at throat of each trap); ammonia (measured at the throat of each trap with an ammonia aquarium test kit). We predicted: 1. Alligator Snapping Turtles would be trapped in areas of greater dissolved oxygen than Eastern Snapping Turtles because they would use areas closer to flowing, oxygen-rich water of main channels; 2. that Eastern Snapping Turtles would be found in more turbid water because of their generalist tendencies and abilities to utilize muddy, backwater pools; and 3. that Alligator Snapping Turtles would not be trapped in areas with as high ammonia as Eastern Snapping Turtles because Eastern Snapping Turtles can adapt to more degraded areas that would exhibit increased ammonia due to run-off or the effects of livestock.

A chi-squared test was used to compare the number of traps that captured only one species of snapping turtle to the number of traps that captured both species of turtle. A discriminant function analysis (DFA) was performed to determine if environmental conditions at traps where Alligator Snapping Turtles were captured differed from sites where Eastern Snapping Turtles were caught; the two species were assigned to two groups *a priori* in the DFA. The DFA is an analysis of the similarity or difference of specified groups as based upon multiple variables. The environmental variables used to determine habitat at trap sites included depth, physical structure in the stream, temperature, detritus, presence of aquatic vegetation, and substrate. When attempting to analyze all variables collected at each trap location, eleven traps were excluded from the analysis due to missing values, and complete DFA results could not be generated. As a result, the above analysis was narrowed to the variables of depth, detritus, temperature, physical structure in the stream, mud or non mud substrate, and aquatic vegetation because values for all of these variables were known at all 59 trap sites. In the summer of 2010, we tested turbidity, ammonia, and dissolved oxygen in addition to the other microhabitat characteristics at each site. In order to examine the importance of these variables in explaining habitats used by the two turtle species, we ran an additional DFA to look at these three variables independently because they had not been gathered in 2009. In order to determine how individual variables differed between sites where turtles were captured, Mann Whitney U -tests were also used to compare if there were significant differences between capture sites of Alligator Snapping Turtles and capture sites of Eastern Snapping Turtles in terms of depth, physical structure, and temperature. For this study, each individual trap set was the experimental unit used for analysis. Only traps that captured either Alligator Snapping Turtles or Eastern Snapping Turtles or both species were used for analysis.

Critical values for significance were set at p=0.05 or less.

All procedures used in our study were in accordance with the SSAR guidelines for field research, and were approved by the IACUC of the University of Missouri-St. Louis and the Missouri Department of Conservation (Univ. of Missouri-St. Louis IACUC Protocol # 09-05-05 and Missouri Department of Conservation Wildlife Collector's Permits # 14134 and # 14548).

RESULTS

Significantly more traps captured only Alligator Snapping Turtles or only Eastern Snapping Turtles than traps that captured both species of snapping turtle (χ^2=55.07, df=1, P<0.001; Figure 2). Additionally, in only one instance were both species trapped in the same trap, and they were not captured on the same day, but 48 hours apart. This was the only case of a capture of both an Alligator Snapping Turtle and an Eastern Snapping Turtle at the same trap location in 557 trapnights during 2009 and 2010.

The Discriminant Function Analysis revealed a significant difference between the locations where Alligator Snapping Turtles were trapped and the locations where Eastern Snapping Turtles were trapped (F=2.097, N=59, P=0.002; Figure 3).

The environment at sites where the two turtle species were captured differed significantly along the first discriminant function axis, which accounted for 94% of the variation (L=0.355, df=12, P<0.001); environmental conditions did not differ as a function of species in the second axis (L=0.912, df=5, P=0.448; Table 1). Alligator Snapping Turtle presence at trap sites was characterized by amount of physical structure in the stream, depth, warmer temperature, and detritus, while Eastern Snapping Turtle presence at trap sites was characterized by aquatic vegetation and mud substrate (Table 2).

When using the variables collected only in 2010 (turbidity, ammonia, and dissolved oxygen) to characterize habitat, the trap locations of Alligator Snapping Turtles and Eastern Snapping Turtles were not significantly different (F=1.831, N=16, P=0.140). Therefore, Alligator Snapping Turtles and Eastern Snapping Turtles did not separate in space based upon these variables.

Univariate analysis of environmental conditions at trap sites reflected DFA results. Alligator Snapping Turtles were trapped significantly more often in sites with greater physical structure, such as many overhanging roots and structure at the surface and underwater (physical structure classified as number 2), while Eastern Snapping Turtles were classified at sites characterized by minimal physical structure (physical structure classified as number 1) (U=195.5, N1=18, N2=42, $P<0.05$; Figure 4). Alligator Snapping Turtles also were trapped in significantly deeper areas than Eastern Snapping Turtles (U=114.0, N1=18, N2=42, $P<0.05$; Figure 5), and they were trapped at significantly warmer temperatures than Eastern Snapping Turtles (U=147, N1=17, N2=42, $P<0.05$; Figure 6).

DISCUSSION

The results of this study demonstrate that within their range in southeastern Missouri, Alligator Snapping Turtles and Eastern Snapping Turtles utilize different microhabitats. Likely as a result of this differential use of microhabitat, these two species were almost never trapped in the same locations.

Santhuff (1993) obtained similar results to our study, in that he did not trap both species of snapping turtles in the same locations, and he did not believe that the two species occurred syntopically. He based this conclusion partly on his previous trapping experience in Florida.

In a recent and, as yet, unpublished study in eastern Texas, Alligator Snapping Turtles also utilized sites with greater depths associated with lotic habitats, while Eastern Snapping Turtles were captured at more lentic sites with greater amounts of emergent vegetation than Alligator Snapping Turtles (Riedle, 2010). Therefore, differential habitat utilization between these two species of turtle appears to extend beyond Missouri.

The reasons for spatial partitioning in the Alligator Snapping Turtle and Eastern Snapping Turtle are arguable, and their differential use of microhabitat may have more than one cause. Alligator Snapping Turtles grow to a much larger size than Eastern Snapping Turtles. The largest Alligator Snapping Turtle trapped in this study was 48.5 kg; the largest Eastern Snapping Turtle was 10 kg. This difference in size may result in the Alligator Snapping Turtles outcompeting Eastern Snapping Turtles for space, food, or other resources in areas where they occur in sympatry.

Territoriality studies involving Eastern Snapping Turtles have shown that home ranges of Eastern Snapping Turtles overlap (Obbard and Brooks, 1981; Kobayashi et al., 2006), which suggests that territoriality is limited. However, overlapping home ranges do not discount the possibility of territoriality within those home ranges. Territoriality in Alligator Snapping Turtles has not been addressed, but male-male combat between individuals prior to mating occurs (Harrel et al., 1996b). Thus, it is feasible that interspecific territoriality may exist between these closely related species, which could lead to habitat partitioning in order to decrease risk of territorial aggression. Nonetheless, at present this possibility remains conjectural because clear-cut evidence does not exist, and the current study did not examine this issue.

Additionally, Alligator Snapping Turtles have been known to consume adult Eastern Snapping Turtles (Shipman, 1993; Pritchard, 2006; Ernst and Lovich, 2009), and agonistic encounters between the two species have been documented in the field, resulting in mortality of two Eastern Snapping Turtles (Shipman and Edds, 1994).

Shipman (1993) also witnessed Alligator Snapping Turtles in captivity kill Eastern Snapping Turtles while other species of turtles (*Apalone spinifera* and *Trachemys scripta*) in the same enclosure remained unharmed. It is noteworthy that in our fieldwork we often trapped Alligator Snapping Turtles with *A. spinifera* and *T. scripta* in the same trap at the same time; however, we never captured *M. temminckii* and *C. serpentina* in the same trap at the same time. It is possible that avoidance of predation and costly aggressive interactions by one species may lead to interspecific resource partitioning (Luicelli, 2008), with Eastern Snapping Turtles occurring in habitats not being used by Alligator Snapping Turtles.

Luicelli (2008) suggested interspecific competition for resources in turtles would be most common in large carnivorous turtles because they face more competition for prey items. The author goes on to predict that future studies will reveal that structures of turtle communities that partition resources will be dominated by two or more large species of carnivorous turtles, such as Chelydridae (Luicelli, 2008).

In our study, the Alligator Snapping Turtle utilized deeper pools, more physical structure in the water column, warmer water, increased detritus, and less aquatic vegetation than the Eastern Snapping Turtle. Thus, habitats that have these characteristics may be colonized by the Alligator Snapping Turtle and possibly defended. In a study on crayfish, Soderback (1991) found the larger and faster-growing crayfish *Pacifastacus leniusculus* to be more aggressive and dominant to the crayfish *Astacus astacus*. The author noted that competitive exclusion may resign one species to inferior or marginal habitats. Some of our trapping results may be consistent with this interpretation: on the Black River we trapped eight Alligator Snapping Turtles in the main channel and only one Eastern Snapping Turtle. On a disconnected old channel that was separated from the main channel trap site only by a levee, we trapped four Eastern Snapping Turtles and no Alligator Snapping Turtles. However, from our results on the Eleven Point River, where we trapped eleven Eastern Snapping Turtles all in the main channel of the river where there were no Alligator Snapping Turtles, it is clear that Eastern Snapping Turtles may also utilize the main channels of rivers. When we did trap Eastern Snapping Turtles in the main channel of rivers, it was almost always in areas where no Alligator Snapping Turtles were trapped. Even on the Current River, where both species were trapped, the Alligator Snapping Turtles were trapped in the channel, while the Eastern Snapping Turtles were trapped further into backwater areas. Because the Eastern Snapping Turtle is widely considered to be a generalist (Moll and Moll, 2004; Riedle et al., 2009), and may utilize a variety of habitats including semi-terrestrial flooded fields and rice paddies, as well as the main channels of streams (Kobayashi et al., 2006), this turtle may reduce competition by switching to marginal habitats away from the lotic stream habitats in areas co-inhabited by the Alligator Snapping Turtle.

Interestingly, one of our findings did not support what has been reported in the literature. In our study, Eastern Snapping Turtles were not associated with physical woody structure in the stream. Eastern Snapping Turtles have previously been reported to prefer physical structure in the water column (Froese, 1978; Ernst and Lovich, 2009), and hatchling Eastern Snapping Turtles have previously been reported to prefer vegetation, in part because of the physical support it provided for them (Sexton, 1958). However, our results show physical structure in the stream was associated with Alligator Snapping Turtles, but not Eastern Snapping Turtles. This, again, may be a case in which Alligator Snapping Turtles are pushing the Eastern Snapping Turtles into less optimal areas with less physical structure in the stream. It is possible that within the sections of stream in which these two species co-occur, physical structure is a limited resource that is sequestered by the Alligator Snapping Turtle, relegating the Eastern Snapping Turtle to suboptimal microhabitats that do not have structure.

Competitive interactions between the Alligator Snapping Turtle and Eastern Snapping Turtle may vary with age and development. This has been observed in crayfish species, in which *P. leniusculus* does not establish dominance over *A. astacus* until later life stages (Soderback, 1991). In captivity, both species of snapping turtles have been housed together in multi-species exhibits, but the Alligator Snapping Turtles outgrow the Eastern Snapping Turtles, and eventually begin attacking them (St. Louis Zoo pers. comm.). Congdon et al. (1992) found that juvenile Eastern Snapping Turtles were found to inhabit shallower areas compared to larger size classes of conspecifics. They speculated that juveniles utilized shallow areas to reduce exposure to predators inhabiting deeper pools of water, including other large turtles. Ontogenetic variation in interspecific competition between turtles may occur in the wild as well, and Eastern

Snapping Turtles may utilize marginal habitats to decrease exposure to adult Alligator Snapping Turtles, but this remains to be tested.

The Alligator Snapping Turtle is listed as a species of conservation concern in Missouri. The causes for decreases in numbers of this species are arguable, but wetlands in Missouri, where *Macrochelys* is found, have been drastically reduced by as much as 93% since the 19th Century (Lescher, Unpubl data). An estimated seventy-seven percent of the wetlands have been converted into croplands (Lescher, Unpubl data). Successful habitat conservation and restoration projects are contingent upon accurate knowledge of what habitats are ideal for the species that is being protected. Based on our data, Alligator Snapping Turtle preservation and restoration projects should include deep pools, abundant physical structure, lack of aquatic vegetation, detritus blanketed substrates, and seasonally variable water temperatures that warm in the summer.

Because it is a game species that is currently harvested in Missouri, the Eastern Snapping Turtle populations may need habitat enhancement now or at some point in the future. Habitat enhancement projects for the Eastern Snapping Turtle should include sites with abundant aquatic vegetation, mud substrates, minimal physical structure, variable depths including shallow wallowing areas, and variable temperatures.

Consideration of the microhabitat characteristics utilized by the Alligator Snapping Turtle and Eastern Snapping Turtle would aid future efforts to conserve Alligator Snapping Turtles in Missouri and could help improve sustainable harvest of the

Eastern Snapping Turtle. Microhabitat is not the sole consideration for successful conservation for turtles, however, and interspecific interactions must be considered, as well. Sections of streams used for such a management effort should include suites of microhabitat favorable to the Eastern Snapping Turtle, and suites of habitat favorable to the Alligator Snapping Turtle.

Future habitat and telemetry studies involving both the Alligator Snapping Turtle and Eastern Snapping Turtle in waters where they co-occur, such as the Current River, are recommended. Such studies would illuminate the dimly visible world of interspecific interactions of Chelydridae. In addition, comparative studies in areas where these species are allopatric are warranted to assess how habitat utilization may be different in such areas. The turtle assemblages in these streams also need to be documented further. This would allow conservationists to maximize efforts to protect Alligator Snapping Turtles in Missouri by providing them with knowledge on what combination of habitat characteristics and turtle interactions are ideal for *Macrochelys* to thrive. They would also generate information on how interspecific competitive interactions affect a game species, the Eastern Snapping Turtle.

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Tables

Table 1. Summary of Canonical Discriminant Functions testing for similarity or dissimilarilty between Alligator Snapping Turtles (*Macrochelys temminkii*) and Eastern Snapping Turtles (*Chelydra serpentina*) characterized by habitat variables at capture sites. Function one was significant while function 2 was not significant. Table of Eigenvalues included.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.568[a]	94.2	94.2	0.781
2	0.096[a]	5.8	100.0	0.297

a. First 2 canonical discriminant functions were used in the analysis.

Table 2. Factor loadings for different variables used to characterize the presence of Alligator Snapping Turtles (*Macrochelys temminckii*) and Eastern Snapping Turtles (*Chelydra serpentina*). Higher absolute value of the loadings indicates the strength of the predictor variable.

Standardized Canonical Discriminant Function Coefficients		
	Function	
	1	2
MUD	-.058	-.001
TEMP AT SET OF NET	.431	-.027
PRESENCE OF AQUATIC VEG	-.597	.682
AMOUNT OF PHYSICAL STRUCTURE IN THE STREAM	.433	.588
DEPTH AT THE THROAT OF THE TRAP	.620	.469
PERCENTAGE OF DETRITUS W/IN 3 M OF TRAP	.318	-.550

Figure Legends

Figure 1. Streams where Alligator Snapping Turtles (*Macrochelys temminckii*) and Eastern Snapping Turtles (*Chelydra serpentina*) were trapped in Missouri during the summers of 2009 and 2010.

Figure 2. Number of traps that captured only Alligator Snapping Turtles (*Macrochelys temminckii*) or only Eastern Snapping Turtles (*Chelydra serpentina*) compared to the number of traps that captured both species in the summers of 2009 and 2010. (x^2= 55.07, n=59, p<0.001).

Figure 3. Discriminant Function Analysis plot of the Alligator Snapping Turtle (*Macrochelys temminckii*) and Eastern Snapping Turtle (*Chelydra serpentina*) trap locations in space. Trap sites where the two species were captured were characterized by differences in water depth, detritus levels, physical structure in the stream, and temperature (See Table 1); the two species were found to be significantly different (F=2.097, N=59, p=0.002). Black triangles indicate Eastern Snapping Turtle trap sites, and open circles indicate Alligator Snapping Turtle trap sites. ASNT refers to Alligator Snapping Turtle. CSNT refers to Eastern Snapping Turtle.

Figure 4. Amount of physical structure in the stream (see text for explananation) at capture sites of Alligator Snapping Turtles (*Macrochelys temminckii*) and Eastern Snapping Turtles (*Chelydra serpentina*). The black line within the shaded box is the median value. The shaded box indicates the 25th percentile through the 75th percentile. The whiskers extending from the box indicate the highest and lowest scores that are not outliers. ($U=114.0$, $n1=18$, $n2=42$, $p<0.05$).

Figure 5. Median depth at trap sites of Alligator Snapping Turtles (*Macrochelys temminckii*) and Eastern Snapping Turtles (*Chelydra serpentina*). The black line within the shaded box is the median value. The shaded box indicates the 25th percentile through the 75th percentile. The whiskers extending from the box indicate where the highest and lowest scores that are not outliers occur. The dots are points over 1.5 box lengths from the 25th or 75th percentile. ($U=114.0$, $n1=18$, $n2=42$, $p<0.05$).

Figure 6. Median temperatures at trap sites of the Alligator Snapping Turtles (*Macrochelys temminckii*) and Eastern Snapping Turtles (*Chelydra serpentina*) in degrees Celsius. The black line within the shaded box is the median value. The shaded box indicates the 25th percentile through the 75th percentile. The whiskers extending from the box indicate where the highest and lowest scores that are not outliers occur. The dots are points over 1.5 box lengths from the 25th or 75th percentile. ($U=147$, $n1=17$, $n2=42$, $p<0.05$).

Figure 1.

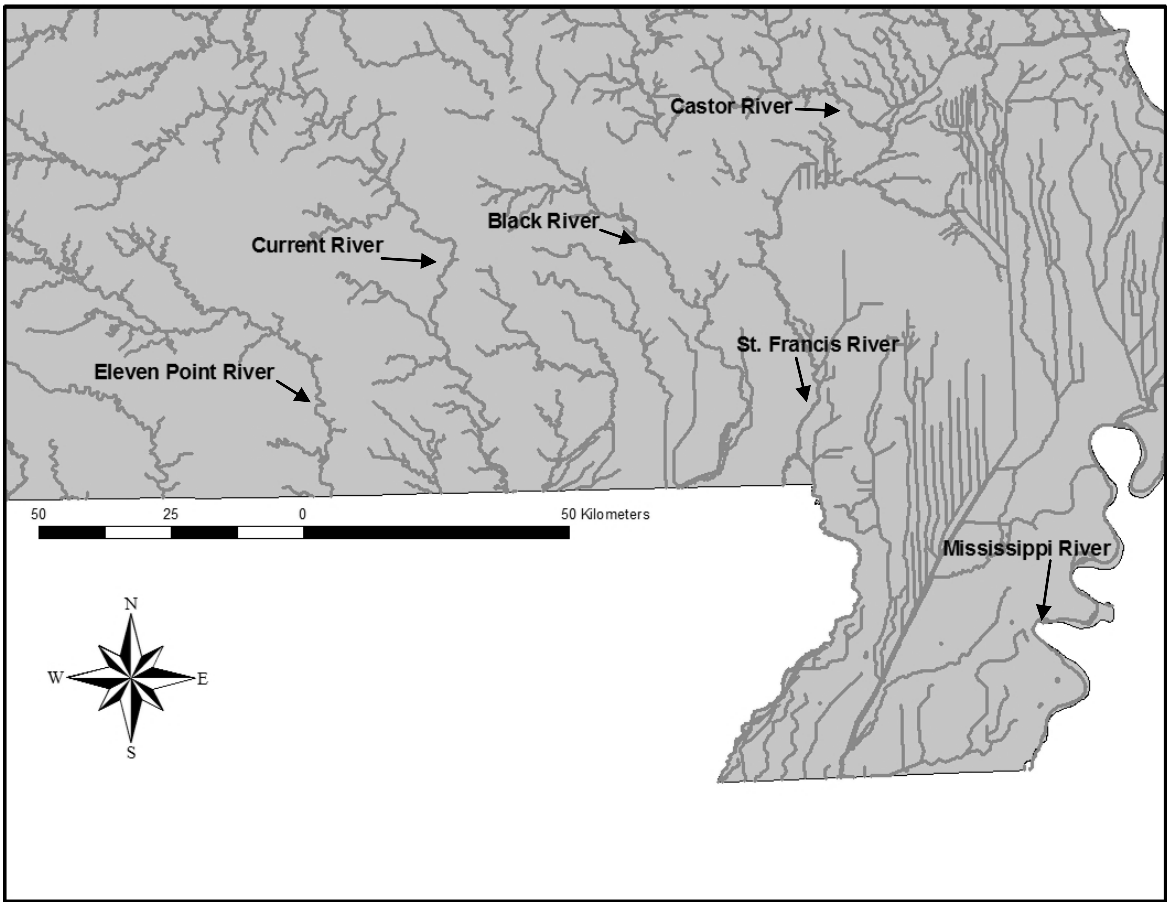

Castor River
Black River
Current River
St. Francis River
Eleven Point River
50
25
0
50 Kilometers
Mississippi River
N
W
E
S

Figure 2.

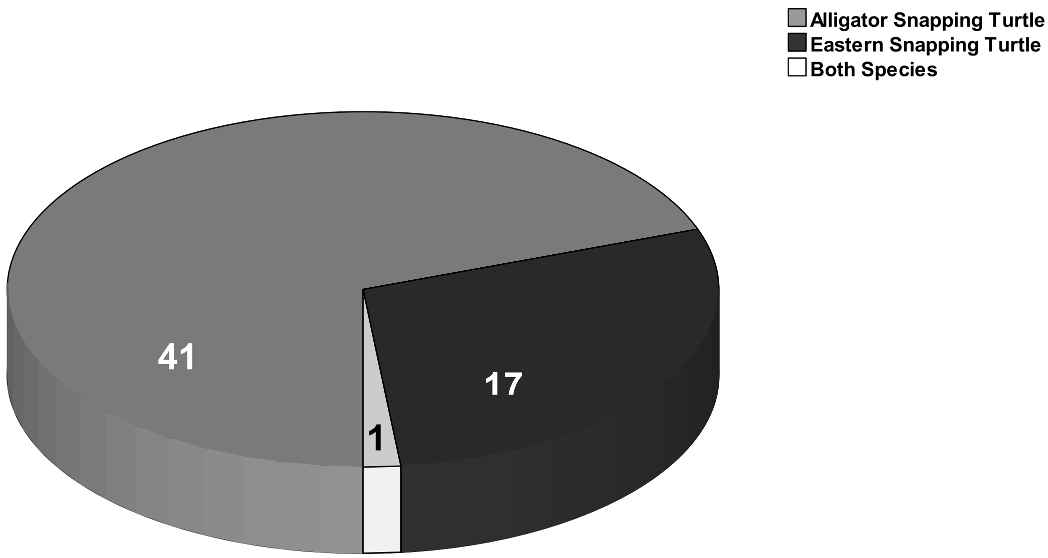

Alligator Snapping Turtle
Eastern Snapping Turtle
Both Species
41
17
1

Figure 3.

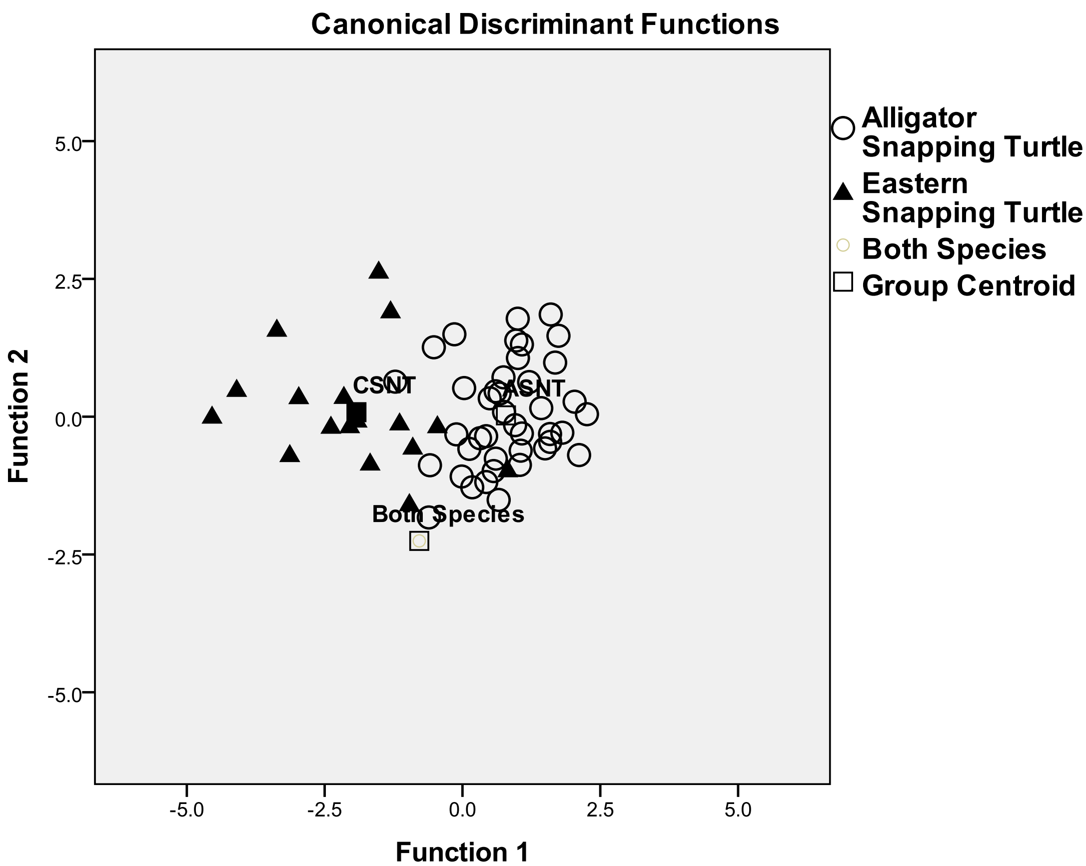
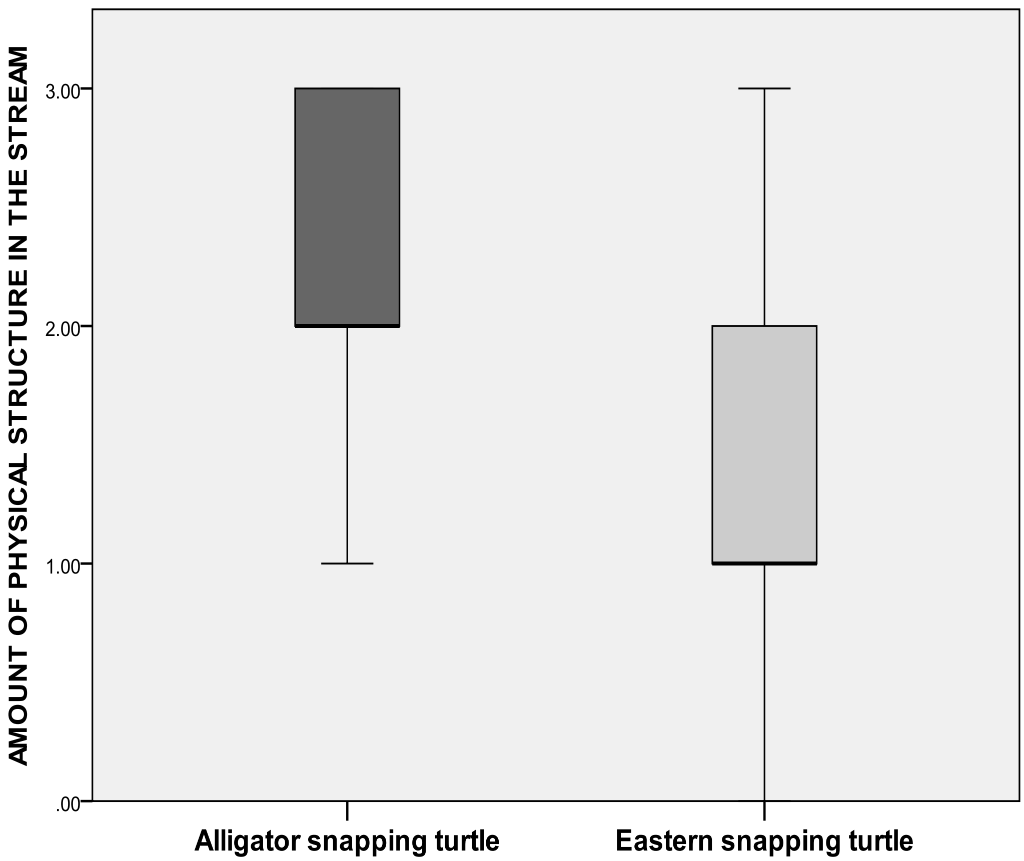
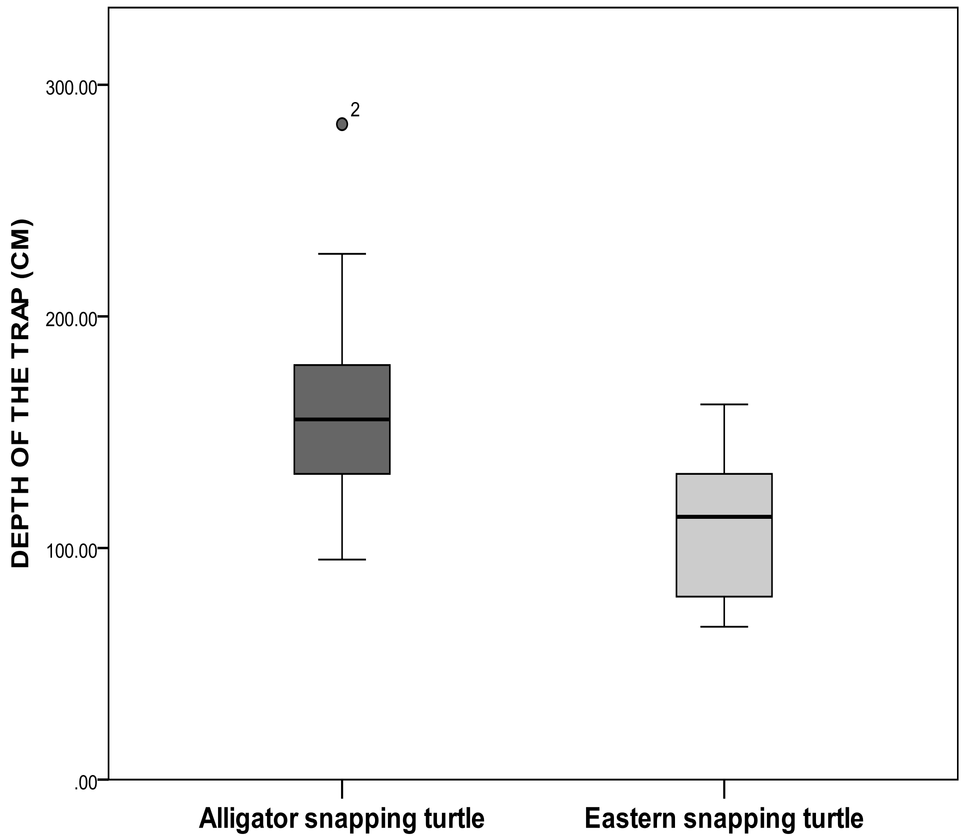

Canonical Discriminant Functions
Function 2
Function 1
5.0
2.5
0.0
-2.5
-5.0
-5.0
-2.5
0.0
2.5
5.0
CSNT
ASNT
Both Species
Alligator Snapping Turtle
Eastern Snapping Turtle
Both Species
Group Centroid

Figure 4.



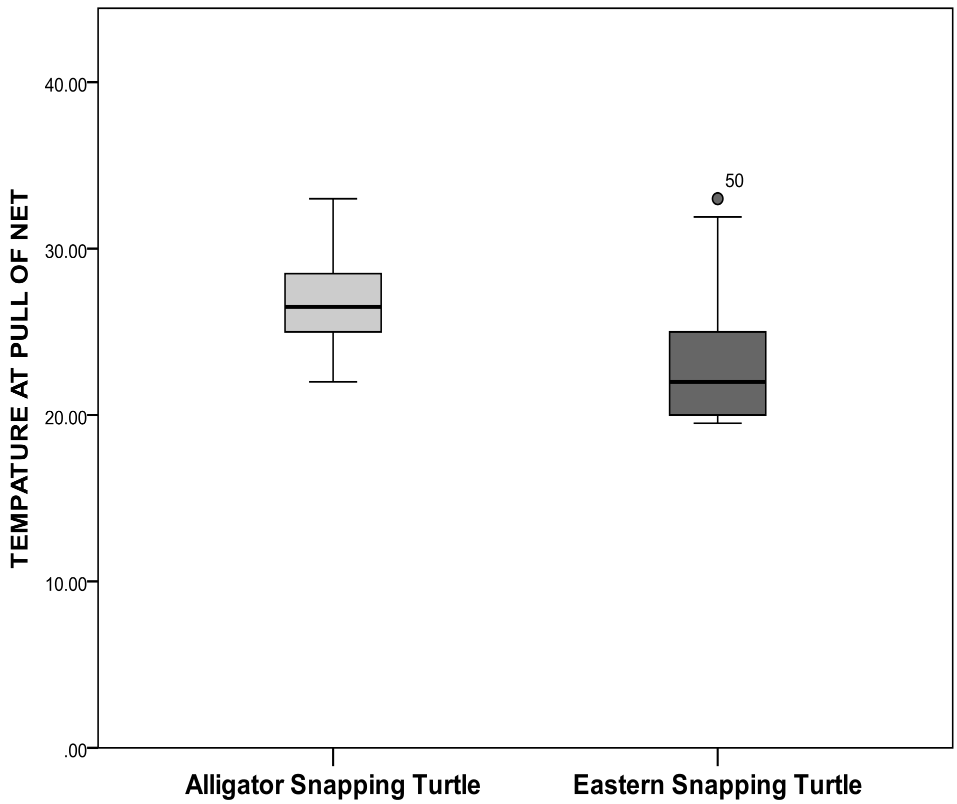
AMOUNT OF PHYSICAL STRUCTURE IN THE STREAM
3.00
2.00
1.00
.00
Alligator snapping turtle
Eastern snapping turtle

Figure 5.



300.00
200.00
100.00
.00
DEPTH OF THE TRAP (CM)
2
Alligator snapping turtle
Eastern snapping turtle

Figure 6.



40.00
30.00
20.00
10.00
.00
TEMPATURE AT PULL OF NET
50
Alligator Snapping Turtle
Eastern Snapping Turtle