RAZOR-BACKED MUSK TURTLE (STERNOTHERUS CARINATUS) DIET ACROSS A GRADIENT OF INVASION

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Abstract.-Diets of freshwater turtles often reflect the availability of food resources in the environment. Accordingly, bottomfeeding turtles' diets are typically composed of benthic macroinvertebrate fauna (e.g., insects and mollusks). However, the composition of benthic systems has changed because many freshwater ecosystems have been invaded by non-native species, including bivalve species such as the Asian Clam, Corbicula fluminea. I studied the diet of Sternotherus carinatus, the Razorbacked Musk Turtle, in southeastern Oklahoma across three zones of Corbicula abundances: no Corbicula, moderate Corbicula densities, and high Corbicula densities. I hypothesized that the composition of Corbicula in the diet would increase with increased abundance of Corbicula in the riverine environment. Turtles were caught by snorkel surveys in the Little and Mountain Fork rivers and kept overnight for the collection of fecal samples. The diet was similar to that found in previous studies on S. carinatus except that Corbicula is a new component of the diet and composed the majority of the diet in high-density Corbicula areas. An Index of Relative Importance (IRI) showed that Corbicula was the most important prey item in the areas with high Corbicula density, was equally as important as gastropods in the areas with moderate Corbicula density, and was absent from the diet in areas without Corbicula. As indicated by a non-metric dimensional scaling ordination, the diet of turtles in the areas without Corbicula was more diverse, containing insects, crayfish, gastropods, unionids, and seeds in high proportions. My data suggest that the diet of S. carinatus has become more molluscivorous and diet diversity has been reduced as the result of the presence of Corbicula.

Key Words.—Corbicula fluminea; invasive species; geographical informational systems (GIS); diet analysis; diet diversity; nonmetric multidimensional scaling (NMDS); Oklahoma

INTRODUCTION

Diets of freshwater turtles often reflect the availability of food resources in the environment. The diet of bottom-feeding turtles is typically composed of the benthic macroinvertebrate fauna, which is often composed of both insects and mollusks (Ernst and Lovich 2009). However, many turtles exhibit some sort of selectivity, by often selecting for particular resources (Mahmoud 1968; Ernst and Lovich 2009). The availability of certain food resources can also be highly influenced by aquatic invasive species and can even lead to shifts in diet (Preston et al. 2012; Rush et al. 2012). For example, female map turtles (Graptemys spp.) have been found to shift their diets to invasive bivalves (Dreissena, Corbicula), thereby reducing dietary diversity (Lindeman 2006a, b; Bulté and Blouin-Demers 2008). The full ecosystem repercussions of invasive bivalves to diet diversity and populations of higher trophic levels are not fully understood.

The Asian Clam (Corbicula fluminea) invaded many water bodies in the southeastern and midwestern United States beginning in the 1950s (McMahon 1982). Corbicula have become a relatively understudied turtle species (Ernst and

large component of the biomass in many freshwater systems (McMahon 1982; Karatayev et al. 2005), but seem restricted to larger, morepermanent bodies of water (Morgan et al. 2003; Karatayev et al. 2005; Sousa et al. 2008). *Corbicula* have been shown to influence nutrient cycling (Atkinson et al. 2010), alter energy flows (Hakenkamp et al. 2001; Sousa et al. 2008; Atkinson et al. 2011), change community composition (Werner and Rothhaupt 2008), and potentially compete with or negatively impact native unionid mussel assemblages (Leff et al. 1990; Cherry et al. 2005; Vaughn and Spooner 2006). While the success of *Corbicula* is evident from their increasing abundance and expanding distributions, their impact on food webs is poorly understood (Vaughn and Spooner 2006). Additionally, previous research has shown that the invasion of *Corbicula* has likely differentially influenced the feeding of benthic freshwater turtles (Lindeman 2006a; Wilhelm and Plummer 2012), thus it is important to study various turtle species.

The Razor-backed Musk Turtle (Sternotherus carinatus) occurs in the deep waters of rivers, streams, oxbow lakes, and swamps, but is a

Lovich 2009). *carinatus* is restricted to the Gulf Coastal Plain and the Ouachita Mountains in Alabama, Arkansas, Louisiana, Mississippi, Oklahoma, Lovich and Texas (Ernst and 2009). Sternotherus carinatus is considered a benthicfeeding omnivore and has been reported to feed on insects, seeds, mollusks, crayfish, carrion, aquatic vegetation, and amphibians (Tinkle 1958; Mahmoud 1968), but has been reported to favor mollusks (Mahmoud 1968). Additionally, previous work has shown that body size can influence feeding preference in that mollusks oftentimes make up a small proportion or mass of younger turtles' diets while adults feed more heavily on mollusks as they get larger (Lindeman 2006a; Ernst and Lovich 2009; Wilhelm and Plummer 2012). It is unclear whether S. carinatus has shifted its diet in response to the introduction of *Corbicula* to river systems, but a preference for *Corbicula* has been reported in a closely related species, Sternotherus odoratus (Wilhelm and Plummer 2012). There have been no diet studies to date on the species since the introduction of *Corbicula* to the geographic range of S. carinatus.

My objective was to describe the diet of S. carinatus in the streams of southeastern Oklahoma across a zone of *Corbicula* invasion and to determine if *Corbicula* has become a main component of the diet. Diet is often reflective of availability of a food resource (Krebs 1989), thus my study encompassed a range of sites that included areas where *Corbicula* has not invaded and areas where *Corbicula* is present. Turtles were captured in each of these habitats allowing me to discern whether S. carinatus was feeding on *Corbicula* and if *S. carinatus* has become more molluscivorous in the presence of Corbicula. In the spectrum of food web studies, this study incorporates knowledge of an understudied species (Lindeman 2008) while incorporating concepts of invasive species ecology and ecosystem change.

MATERIALS AND METHODS

I opportunistically collected turtles between May 2011 and September 2012 during another ongoing project in the Little and Mountain Fork rivers of southeastern Oklahoma, USA. The streams are located in the Ouachita Highland region and contain relatively high species of turtles in areas where *Corbicula* was not

The distribution of the S. richness and densities of native unionid mussels (although distributions are patchy; Matthews et al. 2005). During the study, all sites I snorkeled for turtles were sampled qualitatively (visual snorkel searches) and several sites along a gradient were quantitatively sampled for *Corbicula* presence in 0.25 m^2 quadrats (Fig. 1). It is not clear when *Corbicula* invaded the system, but the first report in the Little River is from 1981 (USGS 2012). Turtles were collected primarily in a 68 km reach of the upper Little River, within which *Corbicula* was not recorded in the uppermost 37 km, but became more prevalent downstream (Fig. 1; mean 30 Corbicula m⁻², range 6.4–63.4 m^{-2}). Additionally, turtles were collected in an 18 km reach of the Mountain Fork River in which *Corbicula* occurs at very high densities (Fig. 1; mean 130 Corbicula m⁻², range 35.2–348 m⁻²). This allowed me to study the diet of *S. carinatus* in areas with no *Corbicula* (upstream portion of the Little River), areas with moderate densities of Corbicula (downstream portions of the Little River), and areas with high densities of Corbicula (Mountain Fork River).

Upon capture, I took standard morphometric measurements and determined sex for all turtles. For each capture location, I recorded the water depth (nearest 0.1 m), substrate type (cobble, gravel, boulder, etc.), and location (UTM coordinates). I kept turtles in tubs or buckets of shallow water (~5 cm) overnight for fecal sample collection. I then filtered samples with a 250 µm sieve and stored in 95% ethanol (Demuth and Buhlmann 1997). I released sampled individuals at their sites of capture within 48 h. I first sorted fecal samples into broad taxonomic categories and then identified items to the lowest classification (Lindeman 2007) possible under a Leica Wild M3Z dissecting microscope (Leica Microsystems, Buffalo Grove, Illinois, USA). I grouped items into 8 categories: unionid mussels, Corbicula, gastropods, insects, crayfish, seeds, leaves, or unidentifiable/other (primarily rocks, sand, and detrital material). Following separation of the groups, I dried each individual sample in a drying oven for 24 hours at 60° C and then determined the dry weight of each dietary item to the nearest 0.0001 g.

Analyses.—To determine if there was a difference in the amount of *Corbicula* in the diets

present or in areas of low or high abundance I divided the site captures into groups: no Corbicula (n = 13), moderate Corbicula densities (n = 14), and high *Corbicula* densities (n = 6). Using a Mann-Whitney Rank Sum Test, I investigated if there was a significant difference in the percentage of *Corbicula* in the diet between the zones with moderate *Corbicula* and high *Corbicula* densities ($\alpha = 0.05$). Using ordinary least-squares (OLS) regression, I also tested for relationships of mass of the fecal sample and the % mass of mollusks (unionid, Corbicula, and gastropods) in the diet with carapace length. The % mass and % frequency were arcsine square-root transformed prior to analysis to meet the assumptions of normality implicit in parametric analyses. The data met the assumption of homogeneity of variance. Additionally, following Lindeman (2006a, b), I calculated a modified index of relative importance (IRI) for each prey category (*i*) as $IRI_i = 100 M_i F_i / \Sigma(M_i F_i)$, where M_i is the mean percentage of the total mass and F_i is the percentage frequency for each prey category *i*. I calculated the IRI for all the turtles sampled and for each category (no *Corbicula*, moderate Corbicula densities, and high Corbicula densities).

To assess diet breadth and overlap, I conducted a non-metric multidimensional scaling (NMDS) ordination using the diet relative abundance data of each turtle to discern dietary similarities and dissimilarities across the site types. Non-metric multidimensional scaling is the most robust unconstrained ordination method (Minchin 1987) and uses occurrence data alone to identify the axes that best explain variation. It seeks an identifiable in their fecal samples and were

pairs of sample variables are in rank order agreement with their dissimilarities in species composition (McCune and Melford 1999). I used the metaMDS function in the vegan package (version 2.0-5; Oksanen et al. 2011) for R (version 2.15.0) with community dissimilarities based on the Bray-Curtis Index. This function produces ordinations based on multiple random starts to avoid local minima and rotates the resulting axes in such a way that the variance between samples is maximized along the first axis. Following the NMDS, I placed convex hulls around the various site types (no Corbicula, moderate Corbicula, and high *Corbicula*) to investigate dietary overlap among the site types. I used a multiple response permutation procedure (MRPP) using a Euclidean dissimilarity index with 1000 permutations in the vegan package to test if there was a significant difference in the groups in multivariate space (Warton et al. 2012). All statistical analyses were performed in R v2.15.1 (R Development Core Team 2012).

RESULTS

Turtle collection.—I caught 37 individuals over the course of this study across the high-, low-, and no-Corbicula abundance habitats. I caught 13 males, 18 females, four juveniles, and two hatchlings during the study, thus the sex ratio was slightly female biased. The mean size and weight of the sexes and age classes is shown in Table 1. The average depth of capture (\pm SE) was 0.77 ± 0.10 m. Four individuals (1 male, 2 females, and 1 juvenile) had nothing or nothing ordination in which the distances between all excluded from the diet analysis. Collectively, 15

TABLE 1. Measurements of average size $(\pm SE)$ with ranges (below) of *Sternotherus carinatus* individuals caught during the study.

Sex/age class	Ν	Carapace length (mm)	Plastron length (mm)	Shell height (mm)	Body mass (g)
Males	13	104.5 ± 7.3	69.9 ± 4.5	51.0 ± 1.3	242.6 ± 16.3
		69.9-128.63	46.2-86.1	45.2-60.9	150.0-330.0
Females	18	98.0 ± 5.0	66.6 ± 3.2	45.5 ± 1.7	177.1 ± 18.2
		66.7-124.1	44.4-82.1	36.4–54.6	110.0-280.0
Juveniles	4	74.1 ± 2.4	53.2 ± 2.5	36.0 ± 0.3	96.6 ± 18.6
		60.5-79.1	41.2-58.1	35.2-36.62	59.8-120.0
Hatchlings	2	49.8 ± 0.8	33.1 ± 0.6	27.8 ± 0.2	28.7 ± 4.5
		48.1-51.5	32.3-33.8	26.7-28.8	28.6-28.8

Atkinson.—Sternotherus carinatus diets across an invasion gradient.

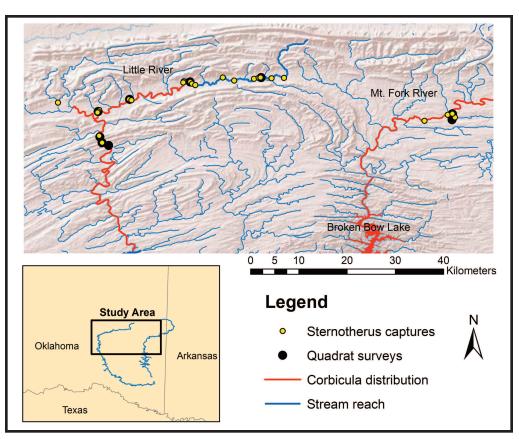


FIGURE 1. Map of the study area showing the known distribution of *Corbicula fluminea* in the rivers and all Sternotherus carinatus capture locations. The reach without Corbicula in the upper Little River (blue) is the zone of no Corbicula, while the reach with Corbicula in the Little River is the zone of moderate *Corbicula* density. All sites in the Mountain Fork River were considered zones of high Corbicula density. Quadrat surveys indicate areas where quantitative samples were taken to determine the density of Corbicula.

turtles were captured in the zone of no *Corbicula* (13 used in diet analyses), 14 in the zone of moderate Corbicula density, and 8 in the zone of the Mountain Fork River where Corbicula high *Corbicula* density (6 used in diet analyses).

Diet.—I collected an average of 0.42 ± 0.06 g of fecal material from individual turtles. In areas without Corbicula, a wide variety of items occurred in the fecal samples: crayfish, dicot seeds, insects, unionids, and gastropods composed the majority of the mass in the individual S. carinatus fecal contents (Table 2; Fig. 2). In the uppermost reaches of the Little River where *Corbicula* was not present, no turtles had *Corbicula* in their fecal samples, while insects, crayfish, gastropods, and unionids were the most frequently found items, respectively (Table 2; Fig. 2B). In the lower portions of the Little River where *Corbicula* were present in moderate densities, insects, of the mass collected was Corbicula. However,

gastropods, and Corbicula were the most frequent items found in their fecal samples. In densities were high, 100% of turtles had Corbicula in their fecal samples, while gastropods and insects made up a smaller proportion of their diet (Fig. 2B; Table 2). The diet item with the highest IRI in the areas without Corbicula was insects (IRI = 38.1; Table 2); trichopteran and chironomid larvae made up the bulk of the insects found. In areas with moderate densities of Corbicula, Corbicula became a large component of *Sternotherus carinatus* diet (IRI = 35.5; Fig. 2A), while gastropods (IRI = 35.5) and insects (IRI = 22.4) remained as large components of the diet (Fig. 2A). The diet of turtles caught in the Mountain Fork River, which had high Corbicula densities, was dominated by Corbicula (IRI = 95.3); on average $83\% (\pm 11\%)$

TABLE 2. Dietary composition of *Sternotherus carinatus* in the Little and Mountain Fork rivers of southeastern Oklahoma. The turtles collected were divided into 3 categories based on *Corbicula* abundance. The %F is the % frequency of turtles that contained a particular diet item, %M is the mean percent mass of the diet item, and the IRI is the Index of Relative Importance.

Prey	<u>No Corbicula</u>			Moderate Corbicula Abundance			High Corbicula Abundance		
Category	%F	%M	IRI	%F	%M	IRI	%F	%M	IRI
Mollusks*	58.3	17.6	15.3	100	50.8	75.6	100	84.2	95.5
Corbicula	0	0	0	45.5	25.4	35.5	100	82.9	95.3
Unionids	25	10.6	8.1	36.4	4.2	4.7	0	0	0
Gastropods	33.3	7.0	7.2	54.5	21.2	35.5	16.7	1.3	0.3
Insects	91.7	13.5	38.1	72.7	10.0	22.4	33.3	11.6	4.5
Crayfish	66.7	15.1	30.9	27.3	0.3	0.2	0	0	0
Seeds	25.0	13.9	10.7	27.3	3.4	2.8	0	0	0
Leaves	27.3	6.0	5.0	0.2	0.9	< 0.1	0	0	0

* Sum of the values for Corbicula, Unionids, and Gastropods

this value is slightly skewed by a hatchling turtle whose fecal contents were 35% *Corbicula*, 58%insect (all trichopteran larvae), and 6.5%gastropod. The diet of all adult turtles (n = 5) caught in the Mountain Fork was > 89%*Corbicula* by mass. If the data on the hatchling are removed, the IRI for *Corbicula* is 95.86 for turtles in the Mountain Fork. Overall, mollusks (unionids, gastropods, and *Corbicula* combined) were an important component of *S. carinatus* diet with summed IRI values of mollusks in the areas of no *Corbicula*, moderate *Corbicula*, and high *Corbicula* being 15.31, 75.64, and 95.54, respectively.

There was a significant difference in the proportion of *Corbicula* found in the habitats of high and moderate *Corbicula* abundance ($U_{20} = 3.0, P = 0.002$), and *Corbicula* was not found in the diet of turtles in the no *Corbicula* habitat. Fecal sample mass was positively related to plastron length ($r^2 = 0.14, y = 0.006x - 0.34, P < 0.05$); however, the % mass of mollusks in the diet was not related to plastron length ($r^2 = 0.14$, y = 0.006x - 0.34, P < 0.05); however, the % mass of mollusks in the diet was not related to plastron length ($r^2 = 0.14$).

Diet Breadth.—The NMDS revealed diet differences through partitioning in diet across the zones of high, low, and no *Corbicula* (Fig. 3). Two NMDS axes explained 96.4% of the variation in diet across the zones. Although NMDS does not give factor loadings, examination of the data indicates that Axis 1 was negatively correlated to *Corbicula* presence in the diet and positively correlated to crayfish in the diet (Fig. 3). The areas of the convex hulls

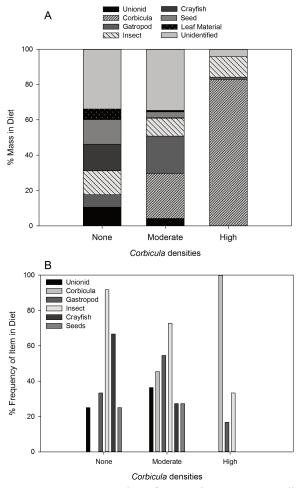


FIGURE 2. Representation of *Sternotherus carinatus* diet. The turtles were separated into categories based on *Corbicula* presence and densities in the habitat. (A) The average percent of mass of the food items in the fecal samples of *Sternotherus carinatus*. (B) The percent frequency of turtles containing a given food item.

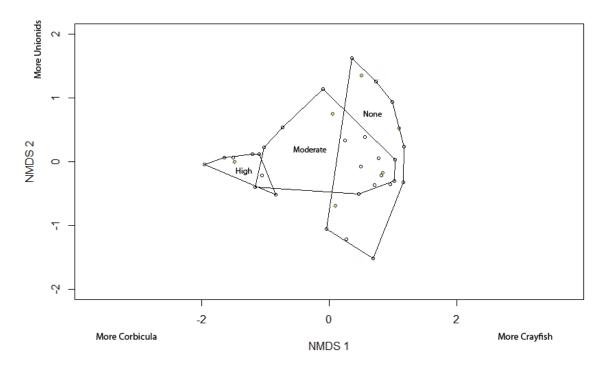


FIGURE 3. Non-metric multidimensional scaling (NMDS) ordination of turtle diet. Convex hulls were drawn around each of the site types: High (high Corbicula densities), Moderate (moderate Corbicula densities), and None (no Corbicula present). Non-dimensional scaling (NMDS) axis 1 differentiated zones with high Corbicula versus crayfish in diets, while unionids in the diet were important in differentiating axis 2.

were greatest for the turtles at the sites of no hatchling turtle's diet in the area of high Corbicula (area = 2.42) and moderate Corbicula density (area = 2.25), but was much lower for the high-density *Corbicula* site (area = 0.31). The MRPP indicated significant differences in the turtle diet across the zones in multidimensional space ($\delta = 1.14$, A = 0.24, P < 0.001).

DISCUSSION

The results of the present study are consistent with previous diet studies on S. carinatus, in that mollusks made up a significant portion of the diet (Mahmoud 1968). However, the mollusks reported by Mahmoud (1968), which is prior to the Corbicula invasion, were almost entirely gastropods. Tinkle (1958) and Mahmoud (1968) both concluded that *Sternotherus carinatus* change from being insectivores to molluscivores as they grow older and larger. However, I did not see a preference for mollusks in larger individuals, perhaps due to the presence of in moderate densities; the convex hull area of

Corbicula density. Mollusks (unionids, gastropods, and Corbicula combined) were an important component of S. carinatus diet, but increased in importance with the presence of Corbicula. I found that in areas with high Corbicula densities, S. carinatus was primarily a molluscivore. My study differs from previous work on *S. carinatus* in that it is the first study of diet on this species following the introduction of *Corbicula* into their habitats and that the study was conducted along a gradient of invasion.

Diet diversity was reduced in areas with high Corbicula densities; all turtles had Corbicula in their fecal samples and it was the most important component of the diet. The NMDS in conjunction with the convex hull analysis showed that turtles in high Corbicula density areas occupied a much smaller trophic space. In contrast, it appears that diet diversity is maintained in areas where Corbicula only occurs Corbicula; Corbicula was also seen in a turtles in the moderate Corbicula density

habitats was similar to the convex hull area of availability of *Corbicula*, but it is not clear if the the turtles in the no Corbicula sites. Almost half of the turtles captured in the moderate *Corbicula* density areas contained *Corbicula* in their fecal samples, yet other items such as gastropods and insects were also prevalent. This species has been characterized as an omnivore that feeds predominantly on insects, snails, and some plant material (Mahmoud 1968), but my results show that S. carinatus that occur in areas with high *Corbicula* densities feed nearly exclusively on this abundant non-native species. These results suggest that S. carinatus have changed their diet substantially since the invasion of *Corbicula*.

The ramifications of the invasion of *Corbicula* for food web structure and nutrient cycling are not fully appreciated. However, it is clear that the invasion has caused diet shifts in many species. For example, Ford and Moll (2004) found that Corbicula occurred in diet of Sternotherus odoratus in a lake, with 17% of turtles having *Corbicula* in their diet. Additionally, Wilhelm and Plummer (2012) found that *Corbicula* occurred in the diet of 57% of individual *Sternotherus odoratus* in a creek system. In the *Graptemys* complex, a switch to a diet in females composed almost entirely of *Corbicula* has been noted in *G. geographica* (Moll 1980), G. versa (Lindeman 2006a), and G. *caglei* (Porter 1990). *Corbicula* has thus become an important energy subsidy for multiple chelonian species. Furthermore, other mollusk invaders such as Zebra Mussels (Dreissena polymorpha) and Quagga Mussels (Dreissena *rostriformis*) have become important dietary items for turtle species such as *Graptemys* spp. and Sternotherus odoratus (Lindeman 2006b; Bulté and Blouin-Demers 2008; Patterson and My results show that Lindeman 2009). *Corbicula* make up the majority of *S. carinatus* diet in areas where Corbicula are abundant and cause a reduction in diet diversity, suggesting that a major diet shift has occurred.

My study did not account for the availability of prey in the system across the Corbicula invasion gradient. Additionally, other sampling techniques (e.g., trapping) may have aided in collecting additional turtles for an increased sample size. However, previous studies on trapping Sternotherus spp. has shown limited success and Sterrett et al. (2010) showed improved capture rates with snorkel surveys of Sternotherus minor. Nevertheless, from my study it is clear that *S. carinatus* responded to the of diet shifts may be greater in other systems.

relative availability of other prey items changed in response to *Corbicula*. Previous studies have found that Corbicula may be competing with or negatively impacting native unionid bivalves (Leff et al. 1990; Cherry et al. 2005; Atkinson et al. 2010, 2011), but their impact on the rest of the benthic macroinvertebrate community is unclear (Werner and Rothhaupt 2008). Given the ability of *Corbicula* to pedal feed (i.e., also able to feed on particles in the benthos; Hakenkamp et al. 2001; Sousa et al. 2008), they could potentially be competing with other macroinvertebrates (Werner aquatic and Rothhaupt 2008). Additionally, the methods for determining diet may have limited my dietary data in comparison to other techniques such as stomach flushing or dissection. In comparison to these other techniques, the method used may have made it difficult to detect soft-bodied organisms that are digested more easily than mollusks. Despite the potential limitation of the method used, dietary results for other *Sternotherus* spp., determined by fecal analysis (Marion et al. 1991), gut dissection (Berry 1975), and stomach flushing (Ford and Moll 2004), have yielded similar qualitative results. Additionally, Lindeman (2007) found that fecal samples were a more accurate description of diet than stomach flushing. Thus, my results are an accurate representation of S. carinatus diet. However, studies in the future would benefit greatly from higher sample sizes and the inclusion of stable isotope analyses to determine the materials that were actually assimilated into tissues by turtles (Phillips et al. 2005; Seminoff et al. 2007).

The first record of the invasive Asian Clam in the lower Little River is from 1981 (downstream from these collections), but earlier reports of Corbiula occurred in Oklahoma in Lake Texoma (Texas border) and Lake Thunderbird in 1975 (USGS 2012). The diet of S. carinatus in the Little and Mountain Fork rivers has likely been influenced by the presence of Corbicula for 25-40 years. Since its invasion, it has become an important prey item for S. carinatus, especially in areas of the Mountain Fork River where it accounts for > 89% of each fecal sample (IRI = 95). The densities of *Corbicula* in my study were not as high as others have reported in other systems (> 2000 clams m^{-2} ; Hornbach 1992; Werner and Rothhaupt 2008), thus the magnitude

Molluscivory has been reported previously for this species (Mahmoud 1968), but it appears that S. carinatus has become more molluscivorous in areas with high densities of Corbicula. The impact of this invasive species is not understood, but it seems to have negative competitive interactions with native unionid bivalves and other macroinvertebrates (Leff et al. 1990; Werner and Rothhaupt 2008; Atkinson et al. 2010) while potentially having positive effects on some macroinvertebrates and aquatic turtle species (Covich et al. 1981; Lindeman 2006a; Wilhelm and Plummer 2012). Future studies incorporating individual and population growth rates in invaded and non-invaded areas would allow a better understanding of the ecosystem impacts of these aquatic invaders.

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