



The importance of turtle populations to wetland restoration in the Upper Mississippi Embayment of the Mississippi Alluvial Valley

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Abstract The Upper Mississippi Embayment (UME) ecoregion covers approximately 141,895 km² and historically supported 9,712,455 ha of bottomland deciduous forests, swamps, bayous, and rivers. Only about 500 ha (< 0.01%) of pre-settlement bottomland hardwood forest habitat in the Mississippi Alluvial Valley (MAV) in the UME remained by the 1940s because the timber was clearcut and the wetlands drained for agriculture. By 1983 only a few scattered cypress-tupelo swamps remained. We studied the freshwater turtle community in Allred Lake, Missouri, a rare remnant of this ecosystem and compared these results to those from two other study sites in the MAV, Big Oak Tree State Park (BOTSP), Missouri, and Coldwater River National Wildlife Refuge (CRNWR), Mississippi. Species richness included six species commonly found throughout the MAV. One species (Red-eared Slider, *Trachemys scripta elegans*) dominated density and biomass in all

three assemblages. The occurrence of the six species we studied in man-made restored wetlands such as those in BOTSP and CRNWR indicate these turtles would adapt to restored wetlands in the MAV in southeastern Missouri and elsewhere in the ecosystem. We provide information on habitat features that could be included in restoration design and construction that would benefit turtles. Given the ongoing worldwide decline of turtles, consideration of turtle ecology and behavior in wetland restoration projects in the MAV may be warranted.

Keywords Biomass · Freshwater turtles · Missouri · Population ecology · *Trachemys scripta elegans* · Wetland restoration

Introduction

To understand the Mississippi Embayment and the Mississippi Alluvial Valley (MAV), it is necessary to examine the lengthy geological history of these areas (Morgan 1983; Van Arsdale and Cox 2007). The Upper Mississippi Embayment (UME) is a physiographic feature and topographically a low-lying basin filled with Cretaceous to recent sediments in the south-central United States. The current sedimentary basin formed by filling a tectonic Cretaceous basin; the UME was a large bay shoreline during the Cretaceous

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to early Tertiary (Van Arsdale and Cox 2007). The Mississippi Alluvial Valley is comparatively recent, created by the Mississippi River and affects seven states, including Louisiana's largest ecoregion of 32,000 km². The region occupied by the UME also occurs within the Coastal Plain Province and is a global biodiversity hotspot (Noss et al. 2014).

At the beginning of the twentieth century, the UME region supported hardwood forested wetlands and vast populations of wildlife, including the ivory-billed woodpecker (*Campephilus principalis*). Over 9 million ha of hardwood floodplain forests occupied the MAV during Pre-Colombian times (Turner et al. 1981; Harris 1984). The MAV covers approximately 141,895 km² and supported 9,712,455 ha of bottomland deciduous forests, swamps, bayous and rivers (<http://mississippialluvialplain.blogspot.com/>, accessed 18 January 2019). In the northernmost MAV, there are 48,369 ha in Missouri, 3739 ha in Illinois, 1682 ha in Kentucky, and 31,922 ha in Tennessee. Conversion of forests to croplands occurred between 1934 and 1990, the majority of which occurred in the MAV during the 1940s through the early 1970s (McWilliams and Rosson 1990). Only about 500 ha (< 0.01%) of pre-settlement bottomland hardwood forest habitat in the MAV within the UME remained after this period (Smith et al. 1993). In northeastern Arkansas, for example, 49,469–86,837 ha of hardwood wetlands were destroyed annually (E. Hanebrink, pers. comm.). By the 1940s, much of the MAV had been clear-cut and drained for agriculture. By 1983, only a few scattered cypress-tupelo swamps of the original bottomland hardwood forest remained.

Beginning in the mid-1970s, a voter initiated and approved 1/8 cent sales tax that funded conservation priorities (Missouri Design for Conservation program) led to the purchase and initial steps of restoring 107,707 ha between 1976 and 1988 (MDC 1988). Much of this land was used for rice crops. By 2012, the combined effort of the Missouri Department of Conservation (MDC)/Ducks Unlimited partnership resulted in restoration of 17,719 ha of wetlands that were primarily designed for wetland waterfowl conservation (MDC 2019a, b). Part of the success is attributed to incorporating 21st century wetland and ecological science into restoration approaches to conservation (Allen et al. 2001). Current restoration projects in southeastern Missouri include 597 ha

during 2016–2025 in the Wilhelmina Conservation Area, Butler and Dunklin Counties (MDC 2016), and 176 ha during 2018–2027 in the Corkwood Conservation Area in Butler County (MDC 2018).

Historically, the MAV in Missouri supported huge populations of turtles, snakes, waterfowl, and other vertebrates. In the nineteen teens, the UME/MAV provided large quantities of freshwater turtles to Chicago where large wholesale markets handled 10,000 snapping turtles per year and 322,958 kg of terrapins (Clark and Southall 1920). St. Louis and Chicago markets were both listed, as was a holding facility near St. Louis at Grafton, Illinois, for up to 1814 snapping turtles and 4000–5000 terrapins. St. Louis had specialty markets for restaurants and many recipes for preparing turtles (Clark and Southall 1920). On 10 June 1960, Herschal Woodruff, who worked for the Memphis Zoo and Max Allen's Zoological Gardens, showed MAN two invoices that documented ca. 907 kg of turtles and 544 kg of snakes he had shipped to a biological supply house in Osh Kosh, Wisconsin. All of them were hand-collected in 2 weeks during construction projects associated with Missouri Highway 51 in Butler County, Missouri. Rather than euthanizing the animals, Herschal agreed to remove and ship them to a commercial business. These invoices provided insights into the number of reptiles from an area that was near our MAV research sites. Habitat loss and collection of turtles for commercial use, especially oriental food markets, has resulted in a precipitous decline in turtles worldwide (Gibbons et al. 2000; Mali et al. 2014; Spencer et al. 2018). Turtles are the most threatened of the major groups of vertebrates, proportionately more so than birds, mammals, fishes, or amphibians (Hoffmann et al. 2010). The nearly complete loss of wetland habitat in the UME contributed substantially to the worldwide decline of turtle populations.

Lovich et al. (2018) reviewed the roles turtles play in aquatic and terrestrial ecosystems. Turtles influence plant community structure (Elbers and Moll 2011), trophic status (Iverson 1982; Congdon et al. 1986), energy flow within and between aquatic and terrestrial ecosystems (Lindsay et al. 2013; Moss 2017), mineral cycling and bioaccumulation (Hinton and Scott 1990), scavenging (Thompson 1993), and soil dynamics (Rogers 1989). The critical roles turtles play in these ecological interactions make this vertebrate group a

necessary component of wetland restoration design and efforts.

The goals of this study were to (1) use capture-mark-recapture data from a study of the turtles in a fragment of a natural MAV bottomland hardwood forest to elucidate community and population structure, (2) compare these results to those from turtle studies in two impacted locations in the MAV and (3) show the value of including these vertebrates in design and construction of restored wetlands in the MAV. Given the ongoing decline of turtles, consideration of turtle ecology and behavior in wetland restoration projects in the MAV may be warranted. We provide information on habitat features that can be included in restoration design and construction.

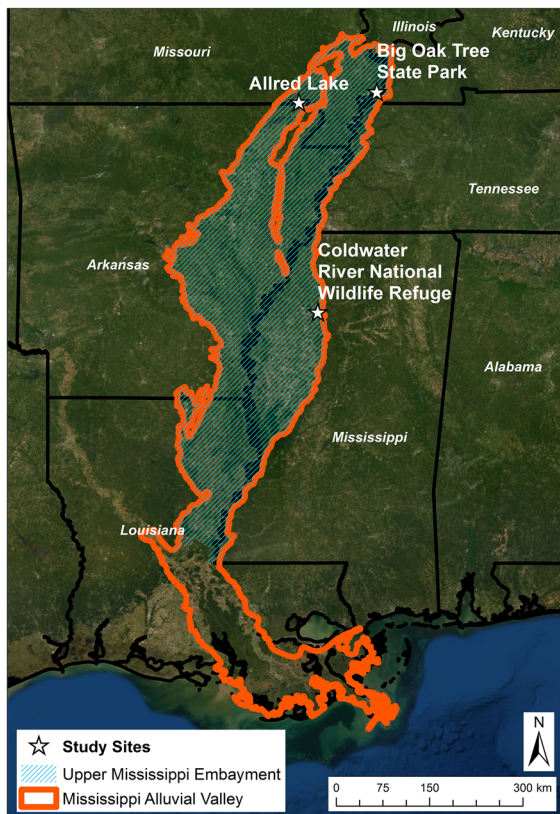


Fig. 1 Location of the three study sites in the Upper Mississippi Embayment within the Mississippi Alluvial Valley. Base map data from Google, 2019

Materials and methods

Study sites

Allred Lake (36.520°N, – 90.416°W, NAD 83; Fig. 1) is in the northwestern region of the UME and part of the Big and Little Hunting Sloughs Area adjacent to the Black River in Butler County, Missouri. Allred Lake appeared to be a component of a natural and near-pristine cypress-tupelo swamp (Fig. 2). Except during droughts, it is connected to the Black River via a relatively dense strip of floodplain forest. At the time of our study, the lake's margins were lined with large bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), black willow (*Salix nigra*), and buttonbush (*Cephalanthus occidentalis*). The water of Allred Lake is usually turbid from edaphic and organic sources and may have reached a depth of 3 m during years of normal rainfall (Janzow and Stauffer 1982). The surface area of Allred Lake varies from approximately 2.5 ha to 7.0 ha; it is not known to completely dry. At the time of our study surface area was estimated at 2.8 ha (J. Wylie, MDC, pers. comm.). The northern side of Allred Lake, the closest point to the agricultural fields at the northern tip of the lake, is about 170 m to the east and 200 m to the north. Allred Lake connects to the Black River through ca. 2 km of lowland forest from the southernmost tip.

Allred Lake had not yet been developed for public access during our 1983 study. The only individuals we encountered were MDC employees. Allred Lake Natural Area contains one of Missouri's best and last



Fig. 2 View of Allred Lake, Butler Co., Missouri, illustrating the shoreline and forest surrounding the lake. Photo by Tom Johnson

cypress ponds in a remnant of the vast network of swamps and bottomland forests that once covered the Mississippi Lowlands of southeastern Missouri. The area is similar to the cypress-tupelo swamps found in Louisiana and other Gulf Coast States (MDC 2019a, b). We conducted the Allred Lake turtle survey during an unusually warm summer coupled with drought conditions between 13 July and 16 September 1983.

In March 2006, the Missouri Department of Natural Resources Water Protection Program updated the Water Quality Certification (RSEIS2) that addressed compensation for the natural resources and environmental impacts within Big Oak Tree State Park (BOTSP; Fig. 1) in Mississippi County, Missouri, by the U.S. Army Corps of Engineers. This included the mitigation/reforestation of bottomland hardwoods in ca. 728 ha of land surrounding BOTSP for a hydrology project. The study area in 2007 consisted of a 9-ha man-made recreational lake constructed on the remains of a bald cypress swamp (Glorioso and Vaughn 2008; Glorioso et al. 2010). The lake was constructed by digging a circular borrow pit, and the excavated earth was used to construct a levee around the pit. The lake fills with groundwater every spring, but the lake and the surrounding shrub swamp dry during droughts. Groundwater is often pumped into the lake in the spring to augment water depth. During restoration, a ditch was constructed to direct water to agriculture lands and, although a levee now closes access to the Mississippi River, extreme floods and agrichemicals may reach BOTSP. The park is separated from all other wooded areas by thousands of hectares in agriculture.

The study area from 2009 to 2011 on Coldwater River National Wildlife Refuge (CRNWR) (Fig. 1), 291 km SSW of Allred Lake, consisted of twenty-three 3–3.6 ha, man-made waterfowl impoundments (formerly catfish ponds) ~ 1.5 m deep each with a weir to control water levels. Two larger ~ 8 ha forested impoundments had been reforested and were not included in the study. Water levels in some ponds were drawn down in spring and summer after the waterfowl had migrated to northern breeding grounds to allow for plant growth, usually a mixture of aquatic grasses, for forage when the birds return in winter. Two of the impoundments were not used and allowed uncontrolled growth of woody plants, primarily black willow. They were not managed for waterfowl, but

water depth varied seasonally and often dry in late summer.

Field sampling

Turtles were trapped in Allred Lake (Fig. 2) during two 3077 trap-hour periods during 13 July to 16 September 1983. Two types of traps were used: commercial, single-throated, 76-cm diameter triple hoop turtle nets and double-throated hoop traps about one-half commercial size. Both traps had 2.54-cm mesh netting. The entire periphery of the lake was trapped using smaller traps in shallow water and commercial traps in deeper water. Each individual trapping event lasted 36 to 72 h. Canned mackerel was initially used as bait for the first trapping session but changed to freshly killed common carp (*Cyprinus carpio*) and shortnose gar (*Lepisosteus platostomus*) thereafter. The survey was conducted in an unusually warm summer coupled with drought conditions.

There were no connections between the lake and other aquatic habitats and it is assumed the populations were closed with no immigration or emigration at the time of our study. We recorded turtle sex using secondary sexual characteristics (Ernst and Lovich 2009), measured maximum straight-line length of the carapace (CL) and plastron (PL) to the nearest mm, weight to the nearest g; individually marked following the procedure introduced by Cagle (1939), and released at the capture site. Few Eastern Spiny Softshell (*Apalone spinifera spinifera*) were captured and only one was measured; it escaped before weighing. Its mass was estimated as the mean mass of three southern Missouri *A. spinifera* of similar carapace length (MAN, unpublished data). Turtles without secondary sex characteristics (e.g., elongated foreclaws) in the emydid genera *Chrysemys* and *Trachemys* were considered juveniles. The Peterson population index, which assumes populations are closed, was used to estimate the population size of the most abundant species, the Red-eared Slider (*T. scripta elegans*), following Overton and Davis (1969) and Donnelly and Guyer (1994).

At BOTSP, Glorioso et al. (2010) used 76-cm and 91-cm three-ring hoop nets baited with sardines as the primary capture technique. Seven to 17 hoop nets were used at any given time and checked at 1–3-day intervals for a total of 37 hoop net checks from 10 June to 27 September 2007. An unbaited 7-ring fyke net

with 7.6-m leads and 6.4-cm mesh was also used for about 5 weeks in July/August 2007. Each captured turtle was identified to species, sexed if possible, measured for straight-line carapace and plastron lengths along the midline, weighed, and individually marked as noted for the Allred Lake study.

Turtles were trapped in CRNWR in Quitman and Panola Counties, Mississippi, during three sampling periods (April, June, September) annually from 2009 to 2011. Standard single funnel, turtle hoop nets (76.2-cm and 50.8-cm diameter traps, Memphis Net and Twine) were baited with partially opened sardine cans to allow bait odor to disperse and used in four impoundments when they held water. The effort was inconsistent among sample periods and limited to those ponds with water deep enough to allow the trap throat to be set below the surface. Hand capture of turtles found terrestrially supplemented trapping. Trapping effort was not standardized, and most turtles were captured haphazardly when not focusing on other aspects of the project. The methods in CRNWR did not allow estimates of density and biomass. We followed the same procedures as described for Allred Lake and recorded sex, carapace and plastron length, and weight. Statistics follow Zar (2009), and significance level was set at 0.05.

Results

We captured a total of 551 individual turtles at Allred Lake in 6154 trap-hours. The two most abundant species were *Trachemys scripta* (77.9%) and Eastern Musk Turtle (*Sternotherus odoratus*; 13.8%; Table 1). Other species captured were Snapping Turtle (*Chelydra serpentina*) (3.8%), Southern Painted Turtle (*Chrysemys dorsalis*; 3.4%), Mississippi Mud Turtle (*Kinosternon subrubrum hippocrepis*; 0.9%) and *Apalone spinifera spinifera* (0.18%). Table 1 includes relative abundance and morphometrics for each species. Sex ratios (M:F) were significantly different for *T. scripta* 1:2.0 (corrected $X^2 = 48.34$, $p < 0.0001$) but not *S. odoratus* 1.2:1 (corrected $X^2 = 0.52$, $p = 0.47$). The structure of the *T. scripta* population indicates robust juvenile recruitment (Fig. 3). A large number (171) of immature females occurred at the time of the study. The population structure for *S. odoratus* indicates low juvenile recruitment; however, small juveniles < 51 mm CL

were not captured due to trap mesh size (Fig. 4). The estimated population size for *T. scripta* was 713 and density was 252.6/ha. We did not calculate population size for *S. odoratus* due to small sample size.

A total of 961 individual turtles of seven species were captured at BOTSP in 2007 (Glorioso et al. 2010). The most abundant turtle by a large margin was *T. scripta*, representing nearly 82% of all individuals captured (Table 1). Other species captured were *C. serpentina* (7.2%), *C. dorsalis* (5.5%), *S. odoratus* (3.2%), *A. spinifera* (2.1%), River Cooter (*Pseudemys concinna*; $< 0.1\%$), and False Map Turtle (*Gratemys pseudogeographica*; $< 0.1\%$). Sex ratios were similar for *T. scripta*, *C. dorsalis*, and *K. subrubrum*, but a male-biased sex ratio was found for *C. serpentina* and a female-biased sex ratio was found for *A. spinifera*. The *T. scripta* population was well represented by adult and sub-adult size classes, indicating repeated successful recruitment. Population density and biomass were dominated in Allred Lake and BOTSP by *T. scripta* (Table 2). The second-most species contributing to biomass for Allred Lake was *A. spinifera*, whereas for BOTSP it was *C. serpentina*.

We encountered the same six species of freshwater turtles in CRNWR as we did at Allred Lake (Table 1). They occupied 9 of the 23 waterfowl impoundments studied. There were 113 total captures of *T. scripta* (87), *K. subrubrum* (14), *C. serpentina* (5), *S. odoratus* (4), *A. spinifera* (2), and *C. dorsalis* (1). The most commonly captured species was *T. scripta*, which occurred in all ponds. Its population structure consisted of 35 adult females, 47 adult males, and 5 immature females and resembled the structure at Allred Lake.

Discussion

The freshwater turtle assemblages in the MAV were dominated by *T. scripta* (Table 1). Species richness and relative abundance of all the turtle species vary among the sampling locations (Table 2). The variation may be due to sampling design and effort, length of study, and differences in habitat structure. The fact that the species assemblage and relative abundance of turtles were similar in three widely separated locations in the MAV indicates this core turtle assemblage was widespread throughout the UME ecosystem prior to

Table 1 Average body size and mass for six species of freshwater turtles in Allred Lake, Missouri, Big Oak Tree State Park (BOTSP), Missouri, and Coldwater National Wildlife Refuge (CRNWR), Mississippi

	Sex	n	PL	CL	Mass	Sex	n	PL	CL	Mass
Allred Lake						CRNWR				
<i>Apalone spinifera</i>	M	3	147.7	204.0	2237.0	M	2	161.0	232.2	–
	F	2	128.5	157.0	987.7 ^b	F	–			
<i>Chelydra serpentina</i> ^a	NS	16	136.9	182.1	1773.0	M	3	228.0	313.0	6686.7
						F	1	214	302	5700
						J	1	153	227	1890
<i>Chrysemys dorsalis</i>	M	13	82.8	91.3	98.7	M	1	110.1	113.5	78
	F	6	88.5	95.1	150.1	F	–			
<i>Kinosternon subrubrum</i>	M	2	73.0	81.0	99.5	M	4	82.7	91.6	138.0
	F	3	90.0	94.0	181.3	F	10	82.7	91.6	162.3
<i>Sternotherus odoratus</i>	M	38	65.7	94.7	135.0	M	4	64.4	86.6	99.4
	F	31	69	93.2	136.0	F	–			
	NS	4	68.2	96.0	134.7					
<i>Trachemys scripta</i>	M	145	129.9	139.9	415.3	M	35	154.0	169.1	651.1
	F	110	169.6	177.2	837.8	F	47	189.9	206.1	1220.6
	ImF	171	108.4	111.8	246.5	ImF	5	132.8	142.8	401.0
	Sex	n	PL	CL	Mass					
BOTSP										
<i>Apalone spinifera</i>		F		15	283.5			403.6		4873.3
		M		5	138.4			200.0		645.1
<i>Chelydra serpentina</i>		F		23	201.9			258.7		4489.1
		M		46	223.9			302.7		6996.6
<i>Chrysemys dorsalis</i>		F		33	127.2			135.4		352.3
		M		20	103.0			111.3		179.4
<i>Sternotherus odoratus</i>		F		12	74.6			97.1		160.8
		M		19	70.4			100.7		172.6
<i>Trachemys scripta</i>		M		397	152.0			167.4		685.2
		F		392	194.8			207.6		1266.7
		ImF		12	125.4			131.1		353.7
		ImM		5	76.2			81.5		91.0

n sample size, *NS* sex not recorded. Carapace length (CL) and plastron length (PL) are in mm and mass is in g. *ImF* immature females, *ImM* immature males, – no captures

^aA few *Chelydra serpentina* from Allred Lake were too large to weigh with our scales. Their weights were estimated from size-weight data in Lagler and Applegate (1941)

^bMass estimated from Lagler and Applegate (1941)

logging and drainage for agriculture. Wetland restoration in the MAV could benefit multiple species.

In BOTSP, Glorioso et al. (2010) found all but one (*K. subrubrum*) of the species that we documented in Allred Lake and CRNWR. Two additional species (*P. concinna* and *G. pseudogeographica*) occurred only in

BOTSP but were uncommon because small ponds and lakes are not their preferred habitat and they are less likely to enter baited traps (Ernst and Lovich 2009). Only two of the former and one of the latter species were captured. Both are known to disperse widely and could have migrated to BOTSP during high water

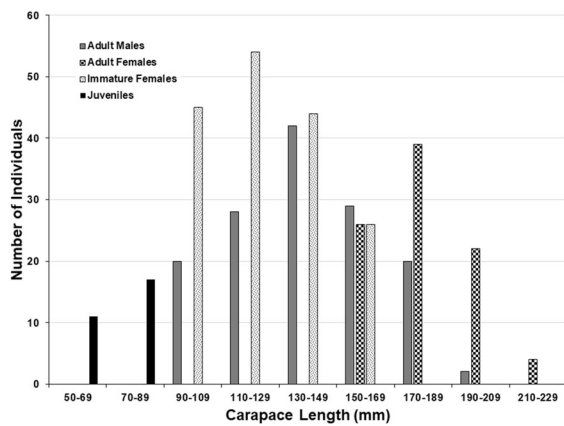


Fig. 3 Structure of the *Trachemys scripta elegans* population in Allred Lake, Butler Co., Missouri

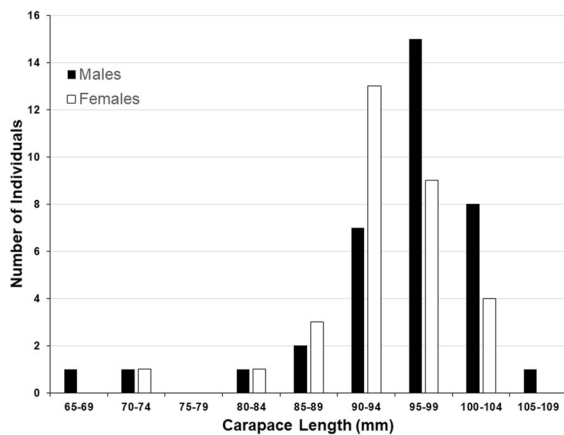


Fig. 4 Structure of the *Sternotherus odoratus* population in Allred Lake, Butler Co., Missouri

events in the Mississippi River (Vogt 1980; Buhlmann

Table 2 Comparisons of population densities and biomass of the freshwater turtles at Allred Lake and Big Oak Tree State Park (BOTSP)

Species	Density (#/ha)		Biomass (kg/ha)	
	Allred	BOTSP	Allred	BOTSP
<i>Apalone spinifera</i>	13.6	1.9	24.1	7.1
<i>Chelydra serpentina</i>	NA	9.3	NA	57.4
<i>Chrysemys dorsalis</i>	12.2	7.9	1.7	2.3
<i>Kinosternon subrubrum</i>	3.1	NA	0.47	NA
<i>Sternotherus odoratus</i>	49.5	25.1	6.4	4.2
<i>Trachemys scripta</i>	279.7	205.8	128.2	178.5

NA not applicable

and Vaughan 1991). Three other species known to occur in the MAV [Smooth Softshell (*Apalone mutica*), Alligator Snapping Turtle (*Macrochelys temminckii*), and Western Chicken Turtle (*Deirochelys reticularia miaria*); Powell et al. 2016] were not found at any of the three study sites. Smooth Softshells occur primarily in rivers and seldom are found in forested wetlands (Ernst and Lovich 2009). The other two species known from the MAV historically are now uncommon (Johnson 2000). *Macrochelys temminckii* is primarily a river turtle but is known to occupy permanent swamps (Ernst and Lovich 2009). *Deirochelys reticularia* occurs in small and often ephemeral ponds, pools, and other shallow bodies of water that often dry in summer months; terrestrial aestivation is common (Buhlmann and Gibbons 2001). This species becomes terrestrial when the ponds dry (Buhlmann 1995; Buhlmann and Gibbons 2001).

Past studies of turtles in the Mississippi River watershed in southern Illinois indicate that freshwater turtle populations in the region were robust. Cagle (1942) studied turtle populations in six diverse aquatic habitats in southern Illinois: two ponds, two lakes, a reservoir lake and a drainage ditch. Species composition was different in each habitat. *Kinosternon subrubrum* was the only species absent from the southern Illinois surveys. Cagle's data estimated *T. scripta* densities in the Carbondale Reservoir at 4.13/ha, but two drying stock ponds had densities of 1000 to 2500/ha. Within the MAV, two aggregations of 1311 turtles were discovered in 250 square meters within a drainage ditch and represented a density of 5.51 turtles/m²; most were *T. scripta* (Cagle 1942). Cagle (1944) also found that open water areas exceeding 1.5 m depth lacking aquatic vegetation were inhabited primarily by large *C. serpentina* and *T. scripta*.

The structure of healthy populations with robust recruitment indicates that energy flow and nutrient cycling in wetlands are functioning naturally (Bury 1979; Lovich et al. 2018). The structure of the *T. scripta* population in BOTSP was similar to Allred Lake with numerous juveniles and subadult female replacements (Glorioso et al. 2010). These age classes will ensure that adult biomass will be maintained at least for this species. Biomass estimates for turtles vary widely (Bury 1979; Iverson 1982). Estimates of 128.2 kg/ha in Allred Lake and 178.5 kg/ha in BOTSP in the MAV for *T. scripta* (Table 2) are higher than for

populations in an Illinois pond (98.5 kg/ha; Reehl et al. 2006), and a Carolina bay (33.6 kg/ha) and small pond (37.1 kg/ha) in South Carolina (Congdon et al. 1986). The turtle assemblage standing crop biomass estimate in Allred Lake (56.8 kg/ha) was considerably greater than that known for populations in the constructed wetlands (27.7 kg/ha) in BOTSP (Glorioso et al. 2010), a 7.3-ha marsh (46 kg/ha) in Michigan (Congdon et al. 1986), and a 1.2-ha cluster of farm ponds (23 kg/ha) in Mississippi (Parker 1990). Biomass for all the turtles in Ellenton Bay (73 kg/ha) and Risher Pond (63.8 kg/ha) on the Savannah River Plant in South Carolina, and a 2-ha pond (142 kg/ha) in Illinois had higher biomass estimates than those obtained for the Allred Lake and BOTSP assemblages (Gibbons 1970; Iverson 1982; Congdon et al. 1986). No density estimates were available for CRNWR. *Trachemys scripta* alone contributed over one-half of the biomass in wetlands where this species occurs.

The occurrence of the six species we studied in man-made wetlands such as those in BOTSP and CRNWR indicates these turtles would adapt to restored wetlands that have been constructed in the MAV in southeastern Missouri and likely elsewhere in the ecosystem. These wetlands are similar in structure and function like the wildlife impoundments in the CRNWR. The relative abundances of these vertebrates revealed in all three of our study locations may have been similar throughout the MAV prior to the massive loss of habitat. Given the many roles these turtles play in freshwater wetlands (Lovich et al. 2018), their presence undoubtedly influenced the trophic structure and energy dynamics in the entire original hardwood forested wetlands in the ecosystem.

The Fish and Wildlife Service impoundment design used for restoration of MAV wetlands works well for migrating birds because the cycle of drawdown with seeding followed by flooding provides resources for overwintering waterfowl. At CRNWR, drawdown occurs March–July and pond refill occurs in fall months; standing water is present in winter months (B. Rosamond, USFWS, pers. comm.). Freshwater turtles that colonize these impoundments are not subject to exposure to freezing temperatures. When these ponds dry the following summer, turtles move to other ponds with standing water. When all the ponds become dry, as occurred on CRNWR in the third year of study, turtles moved to the adjacent ditch that held water even during drought periods. A nearby water body

would assure that turtles in the impounded restored area would be able to recolonize the ponds once they refill. Turtles in restored wetlands that are drawdown completely in winter are subject to freezing and mortality from predation by raccoons, otters, and herons (Ernst and Lovich 2009). Another source of mortality in addition to that of adults is predation of eggs in nests. Mortality can be as high as 100% in some years (Tinkle et al. 1981; Congdon et al. 1983). Construction of nesting areas with suitable soil and protective barriers have been used successively for Wood Turtles (*Glyptemys insculpta*) in New Jersey (Buhlmann and Osborn 2011) and Diamond-backed Terrapins (*Malaclemys terrapin*) in coastal Georgia (Quinn et al. 2015) to mitigate high mortality rates of eggs. A basic understanding of reptile ectotherm biology, like turtles, to predict the effects of changing environmental conditions and predation is essential for restoration managers.

Impoundment design features that include slope angles that allow turtles to crawl out would be beneficial. Once the berms have been implemented, then installation of woody debris (log and limb piles) would provide basking sites and underwater refugia. Aquatic vegetation would provide a food source for the omnivores (*T. scripta*, *C. serpentina*, *C. dorsalis*). The vegetation would then be colonized by snails and provide a food source for the carnivores (*A. spinifera*, *K. subrubrum*, *S. odoratus*; Ernst and Lovich 2009). Aquatic vegetation in the ponds and around the margins would have a positive cascading effect by attracting invertebrates and frog predators along with their primary predators, snakes and herons. Restoration of MAV wetlands by creating waterfowl-like impoundments can only partially replace or mimic the original wetland habitats. Many species of waterfowl occupy these wetlands for only a portion of the year, whereas freshwater turtles are permanent residents. Omission of this group of vertebrates and their many functions in restoration design and construction would mean that restored wetlands in the UME region will never be able to match the original natural habitats. The occurrence of many of the turtles in national wildlife refuge waterfowl impoundments shows that incorporating turtle ecology into restoration efforts could improve the habitat for more vertebrate groups in the MAV. Understanding turtle behavior, life histories, and habitat use of each species could point to practical landscape modifications for species in

addition to waterfowl. Such modifications would not require additional substantial efforts by managers and construction crews. The habitat management guidelines in Bailey et al. (2006) and Kingsbury and Gibson (2012) would be useful resources for wetland restoration design and implementation for turtles, amphibians, and reptiles.

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