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## ASSEMBLAGE STRUCTURE OF AN EASTERN TEXAS AQUATIC TURTLE COMMUNITY

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**Abstract.**—In recent years there has been a significant increase in our knowledge of global and regional patterns of turtle diversity. Species assemblage patterns are thought to be predictable across larger geographic scales, although there is still much to learn about assemblage patterns at local scales. Previous null model testing of aquatic turtle assemblages suggested that microhabitat and food were important dimensions in determining turtle community structure, but more data are needed to refine our understanding of their assemblage patterns at local and regional scales. We sampled for aquatic turtles at Gus Engeling Wildlife Management Area (GEWMA) in eastern Texas, USA, between 2007 and 2009 to test for species segregation along environmental gradients and between macro-habitats. We captured eight species of aquatic turtles at GEWMA, which segregated along environmental gradients based on stream flow, depth, availability of basking structure, and percentage of emergent vegetation. We also observed segregation among macrohabitat types between closely related species of both chelydrids and kinosternids.

**Key Words.**—community ecology; emydids; kinosternids; chelydrids

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### INTRODUCTION

Ecologists have long been interested in how factors like biogeography and niche relationships interact to create patterns of turtle diversity. Globally, turtle species richness is greatest within the lower Ganges-Brahmaputra River Basin in India (23 species) and the Mobile River Basin in Alabama, USA (19 species; Iverson 1992; Buhlmann et al. 2009). In the USA, partitioning within and between northern and southern species assemblages in regions of sympatry has been documented, suggesting little exchange in species on large regional scales (Moll and Moll 2004; Dreslik and Phillips 2005). In the southeastern USA, high species richness patterns are related to high rates of speciation within the Emydidae and Kinosternidae, resulting in smaller geographic range sizes, and increasing regional, but not local species diversity (Stephens and Wiens 2003). Local species pools are generally restricted to specific river drainages reducing interactions on larger geographic scales. Within drainages, species tend to show strong segregation between (Anderson et al. 2002; Dreslik and Phillips 2005) and within (Bodie et al. 2000; Lindeman 2000) lentic and lotic environments. Turtles within the genera *Graptemys* and *Apalone* tend to dominate lotic habitats; whereas, Sliders (*Trachemys scripta*), Common Snapping Turtles (*Chelydra*

*serpentina*), and Common Musk Turtles (*Sternotherus odoratus*) primarily occurred within more lentic sloughs and oxbows (Bodie et al. 2000; Anderson et al. 2002; Dreslik and Phillips 2005).

Community structure at local scales can be explained by differences in habitat associations among species. Ultimately, adaptation of species to biotic and abiotic conditions results in a fit between the organism and its environment, which fundamentally influences local community structure (Losos 1996; Stephens and Wiens 2004). Understanding the roles of local and regional factors influencing local richness is integral to developing conservation strategies for species and ecosystems. For many taxa, such as turtles, that have undergone world-wide declines (Klemens 2000), local patterns of community structure are still poorly understood.

Luiselli (2008) tested for non-random patterns in freshwater turtle community structure using null models based on data from the peer-reviewed literature. His results suggested that community structure was non-random, and that microhabitat and food were the two most important dimensions in determining community structure in turtles. Three regional studies of turtle communities demonstrated predictable patterns in turtle assemblages over larger scales based on habitat relationships (Donner-Wright et al. 1999; Dreslik and

Phillips 2005; Riedle et al. 2009). Within those studies, species assemblages could be categorized as lentic or lotic communities, although there may be seasonal shifts in assemblages as scarcity of permanent water in lentic habitats results in mixing of species in lotic habitats (Bodie and Semlitsch 2000; Bodie et al. 2000; Anderson et al. 2002). To better understand how local scale processes influence the structure of turtle communities, more empirical testing is needed. We sampled one site in east Texas from 2007 to 2009 to determine the degree of overlap of use of macrohabitats and to test for segregation of turtle species along environmental gradients.

#### METHODS AND MATERIALS

**Study area.**—Our study area was located in Anderson County, Texas, USA, on the Gus Engeling Wildlife Management Area (GEWMA) managed by the Texas Parks and Wildlife Department (TPWD). GEWMA is a 4,434-ha property encompassing a large portion of Catfish Creek, a major tributary of the Middle Trinity River Basin. Twenty-four small creeks feed Catfish Creek, most of which are spring fed. Habitat associated with the Catfish Creek ecosystem is characterized by Post Oak (*Quercus stellata*) savanna, bottomland hardwoods, marshes, swamps, bogs, and springs. Aquatic habitat at GEWMA is represented by Catfish Creek and its tributaries, adjacent scours and backwater habitat, open canopy marshes, several small ponds and larger lakes. Aquatic habitat along Catfish Creek is augmented by a series of levees and flood control gates, built in cooperation with Ducks Unlimited, to provide seasonal wetlands and green tree swamps for waterfowl. In addition, there are several ponds or borrow pits associated with the levees (Eric Wolverton, pers. comm.).

**Sampling.**—Trapping methods for aquatic turtles can show biases in captures among species, age classes, and sexes (Cagle and Chaney 1950; Ream and Ream 1966; Koper and Brooks 1998). To more completely sample aquatic habitats at GEWMA, we used seven types of trap gear, and sampled between mid-April and late July, 2007–2009. Trap gear consisted of two sizes of fyke nets, two sizes of hoop nets, two sizes of collapsible box traps, and one size of sea bass/dome traps. The large fyke net (Christensen Nets; Everson, Washington, USA) was 4.5 m in length (front frame to cod end) with a single 14.5 m × 88 cm lead. The two anterior rectangular frames were 120 cm × 88 cm followed by five, 88-cm diameter round hoops, with three 3-cm diameter stretchable funnels leading to the cod end. Square mesh size was 1 cm. The smaller fyke net (Christensen Nets; Everson, Washington, USA) was 3.3 m in length from the front frame to cod end, and had a

single 7.4 m × 67 cm lead. The two rectangular front frames were 95 cm × 67 cm, followed by four 67 cm diameter hoops. Both fyke nets had a single vertical slit funnel within the rectangular frames. There were two 31-cm diameter stretchable funnels leading to the cod end with a square mesh size of 1 cm. The larger hoop (Memphis Net and Twine; Memphis, Tennessee, USA) consisted of three 88-cm diameter metal rings and one 31-cm diameter stretchable funnel. Overall trap length was 245 cm and the square mesh size was 2.5 cm.

We purchased collapsible box traps and sea bass traps from Memphis Net and Twine (Memphis, Tennessee, USA). The mini catfish hoop net had four 47-cm diameter fiberglass hoops, two 27-cm diameter stretchable funnels, and an overall length of 155 cm (square mesh size 2.5 cm). Small box traps were 59 cm × 43 cm × 22 cm, with a square mesh size of 1 cm. There was a 43-cm, horizontal-slit funnel opening on opposite ends of the long axis of the trap. Large box traps were 79 cm × 60 cm × 25 cm with a square mesh size of 1 cm, and had a 60-cm horizontal-slit funnel on opposite ends of the long axis of the trap. Dome traps were 96 cm × 64 cm × 61 cm. Square mesh size was 2.5 cm and there were two 15-cm rigid funnels (funnel held open with a plastic ring) located on each end of the trap.

We baited traps with sardines and fresh fish, used both singly and in combination depending on availability. The number of traps set during each trapping season was dependent on availability, which was driven by cost, as traps ranged from US \$30–1,100 depending on trap type. We set all trap types in all available habitats, although the number of each trap type used during a trapping session was dependent upon variables such as depth and flow (Riedle 2014). We checked traps at least once every 24 h, with trap sets usually completed by early-late afternoon and checked by late morning of the next day. Sampling gear was set so that some portion was exposed above the water surface, providing air space for turtles and other air breathing organisms.

**Community analysis.**—To measure the relative amount of habitat overlap between species at GEWMA, we used Pianka's Index of Niche Overlap (Pianka, 1973):

$$L = \sum_{i=1}^s P_{iA}P_{iK} / \sqrt{P_{iA}^2 P_{iK}^2}$$

where  $P_{iA}$  and  $P_{iK}$  represent proportional habitat use of one species (A) to a second species (K), and  $S$  is the number of species. We calculated niche overlap using EcoSim (Gotelli and Entsminger 2001). We characterized habitat types as: Creek (flowing waters associated with Catfish Creek and its tributaries); Backwater (scours and flooded timber associated with the Catfish Creek floodplain); Marsh (shallow, open

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**TABLE 1.** Total number of trap nights by trap type and macrohabitat at Gus Engeling Wildlife Management Area, Anderson County, Texas, USA (2007–2009).

Trap Type	Habitat Type				
	Creek	Backwater	Marsh	Pond	Lake
Large Fyke	12	32	5	13	5
Small Fyke	9	22	10	8	3
Mini-hoop	11	21	5	15	7
Large Hoop	166	95	6	26	22
Large Box	42	271	97	84	24
Small Box	12	110	34	27	8
Dome	16	6	6	9	0

**TABLE 2.** Catch per unit effort (turtles/ trap night) by habitat type at Gus Engeling Wildlife Management Area, Anderson County, Texas, USA (2007–2009).

Species	Total Captures	Creek	Backwater	Marsh	Pond	Lake
Common Snapping Turtle	21	0.01	0.02	0.01	0.05	0
Alligator Snapping Turtle	12	0.03	< 0.01	0	0	0.01
Eastern Mud Turtle	21	0	< 0.01	0.10	0.00	0.00
Razorback Musk Turtle	40	0.12	0.03	0	0	0
Common Musk Turtle	19	0.03	0.02	0.02	0.01	0
Spiny Softshell Turtle	7	0.02	< 0.01	0.01	0.01	0
River Cooter	3	0	< 0.01	0	0	0
Slider	366	0.05	0.42	0.23	0.59	1.10

canopy, heavily vegetated water bodies associated with smaller feeder creeks, springs and bogs); Pond (small manmade water bodies and borrow pits  $\leq 100$  m diameter); or Lake (larger, several ha manmade water bodies).

To address important biotic and abiotic factors driving community composition of aquatic turtles at each trap set, we measured a suite of five structural variables: canopy cover, depth, flow, basking availability, and emergent vegetation. We recorded canopy cover at the trap using a concave forestry densiometer (Lemmon 1957). We recorded depth at the opening of the trap gear. We also recorded flow at the opening of the trap gear using a handheld flow meter (Global Water; College Station, Texas, USA) averaging current speed at five points within the water column. We recorded basking site availability as the percentage of exposed surface (bank, emergent woody debris) present within a 25-m radius surrounding the trap. We recorded emergent vegetation as the percentage of aquatic vegetation present within a 25-m radius area surrounding each trap.

We ran a series of ordination analyses to determine species distributions along environmental gradients based on abundances of each species within each net. To detect species segregation without the direct influence of environmental gradients that we measured, we first used Correspondence Analysis (CA), a form of indirect gradient analysis (ter Braak and Prentice 1988; Palmer 1993). Assuming that turtles segregate along environmental gradients, one should detect species patterns across a hypothetical space represented by the distribution of sites (traps). Thus, spacing of species

within a CA output represents the amount of change or beta diversity along a gradient.

We then used Canonical Correspondence Analysis (CCA), a direct gradient analysis (Palmer 1993; ter Braak and Verdonschot 1995), to relate species patterns to environmental variables. Canonical Correspondence Analysis is a multiple linear least-squares regression where the site scores, determined from weighted averages of species, are the dependent variables and the environmental variables are the independent variables (Palmer 1993). Canonical Correspondence Analysis allows one to examine the effect of environmental variables on patterning communities. However, the results from a CCA are dictated by the environmental variables chosen. In contrast, because CA is an indirect gradient analysis, it allows one to pattern communities and infer how these communities are structured based on a set of measured environmental variables or other factors that were not measured (Palmer 1993). We performed both CA and CCA using CANOCO version 4.5 (ter Braak 1987). Monte-Carlo permutation tests were run to identify which of the measured variables were the most important in determining the ordination.

## RESULTS

We sampled Gus Engeling WMA for 1,239 net nights (Table 1) making 489 captures of eight species of turtles (Table 2). Although we observed River Cooters (*Pseudemys concinna*) basking in open marshy areas quite frequently, they were highly under-represented in capture data. Because of the disproportionately low captures of River Cooters, this species was excluded from our analyses. Catch per unit effort for all species

**TABLE 3.** Pianka indices for niche overlap (Pianka, 1973) based on five macrohabitat variables for turtle species at Gus Engeling Wildlife Management Area, Anderson County, Texas, USA, 2007–2009.

	Common Snapping Turtle	Eastern Mud Turtle	Alligator Snapping Turtle	Common Musk Turtle	Razorback Musk Turtle	Slider
Spiny Softshell Turtle	0.538	0.289	0.937	0.765	0.921	0.376
Common Snapping Turtle		0.352	0.435	0.757	0.513	0.900
Eastern Mud Turtle			0.109	0.407	0.149	0.403
Alligator Snapping Turtle				0.805	0.984	0.378
Common Musk Turtle					0.878	0.778
Razorback Musk Turtle						0.454

were low at this site, but we did notice habitat specific patterns in capture rates for some species (Table 2). Capture rates for Common Snapping Turtles were slightly higher in pond habitats than in other habitats, while Alligator Snapping Turtles (*Macrochelys temminckii*) had slightly higher capture rates in creek habitat (Table 2). Eastern Mud Turtles (*Kinosternon subrubrum*) were predominantly captured in marsh habitats, and Razorback Musk Turtles (*Sternotherus carinatus*) in creek habitats; however, capture rates were fairly even across all habitats but lakes for Common Musk Turtles (Table 2). Sliders had very low capture rates in creek habitats and highest capture rates in lake habitats (Table 2).

Niche overlap values range from 0.0–1.0, with higher values reflecting increasing overlap of resources. Overlap of resource use was high among Alligator Snapping Turtles, Spiny Softshell Turtles (*Apalone spinifera*), and Razorback Musk Turtles (Table 3). A similar degree of overlap was also seen between Sliders and Common Snapping Turtles (Table 3). Common Musk Turtles had moderate to high overlap with all species, while Eastern Mud Turtles had low overlap with all species (Table 3). Among the three species of Kinosternidae that were captured, Common Musk Turtles overlapped considerably in use of habitat with Eastern Mud Turtles and Razorback Musk Turtles, while Razorback Musk Turtles and Eastern Mud Turtles overlapped very little in habitat use. The two species of chelydrids, Common Snapping Turtles and Alligator Snapping Turtles, had only a moderate degree of overlap in habitat use (Table 3).

Correspondence Analysis resulted in clustering of five species (Slider, Common Musk Turtle, Common Snapping Turtle, Razorback Musk Turtle, and Spiny Softshell Turtle) with low scores on the first and second axes (Fig. 1). Eastern Mud Turtles had higher scores on the second axis, and Alligator Snapping Turtles higher scores on the first axis (Fig. 1). The inclusion of measured environmental variables within a CCA resulted in a strong gradient influenced by flow, depth, and basking structure, and a secondary gradient influenced mostly by emergent vegetation and canopy cover (Fig. 2). The percentage variance explained by the

species-environment relationship for the first two axes was 78.4%, and the addition of the third and fourth axes explained an additional 17% of overall variance. Sliders and Common Musk Turtles occupied sites with minimal depth and more basking structure. Common Snapping Turtles were more common at sites with intermediate depth and emergent vegetation. Eastern Mud Turtles occupied sites with shallow water and high percentages of emergent vegetation. Razorback Musk Turtles, Alligator Snapping Turtles, and Spiny Softshell Turtles occupied sites with greater depth and increasing flow. Locations of species scores represented a transition of species among lentic and lotic habitats, with more emergent vegetation and decreasing depth separating both lentic habitats and the species associated with lentic habitats (Fig. 2).

## DISCUSSION

The sampling techniques we used were adequate for detecting species occurrence with enough sampling effort, although River Cooters were highly under-represented in our samples. River Cooters do not appear to be easily attracted to bait or do not enter traps very readily, and the resulting disparity in number observed vs. number trapped seems to be a trend in other studies as well (Lindeman 2001; Lindeman and Scott 2001). Use of multiple trap types allowed us to more easily sample multiple habitat types, each of which varied in depth and flow. Overall composition of captures in the most frequently used traps (fyke nets, large hoop nets, large box traps) were similar, although the order and rate of species captured varied by trap type (Riedle 2014).

Correspondence Analysis resulted in a clustering of several species at Gus Engeling WMA. Although each of these species has specific habitat requirements, they overlapped in their use of available habitats at this site. The exception was the Eastern Mud Turtle, which was largely restricted to shallow, heavily vegetated habitats, a pattern reported in other studies (Buhlmann and Gibbons 2001). The location of the species score for Alligator Snapping Turtles was intriguing. Although this species shared habitat with several other species, they were segregated from the others along Axis 1.

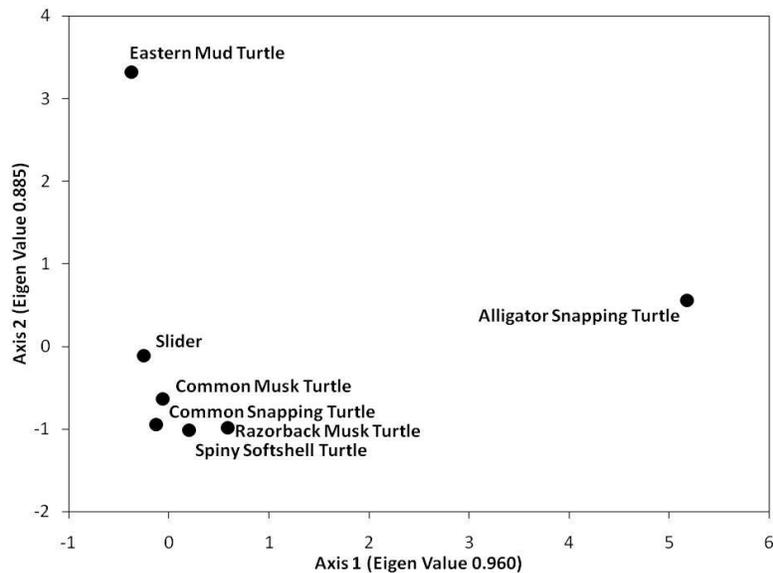


FIGURE 1. Distribution of species scores based on the first and second axes from Correspondence Analysis for aquatic turtles at Gus Engeling Wildlife Management Area, Anderson County, Texas. Total inertia for all axes is 4.98.

Alligator Snapping Turtles consume a wide variety of prey, including other species of turtles (Pritchard 1989; Ernst and Lovich 2009) and agonistic/predatory behavior towards large individuals of Common Snapping Turtles has been reported (Shipman et al. 1994). Because individual nets were considered a site within our analyses, the presence of a large predatory turtle within a net (or site) could have excluded other turtles (Cagle and Chaney 1950), thus skewing the results of the CA.

The Canonical Correspondence Analysis results largely match what is known about the natural history of the various species. Sliders are considered ecological generalists and are typically captured in many aquatic habitats (Ernst and Lovich 2009). Within our ordination analyses, Sliders were positioned fairly close to the origin of both axes, suggesting that outside of possibly basking structure, they were not selecting any particular habitat. Spiny Softshells mostly inhabit river and stream channels (Vandewalle and Christiansen 1996; Bodie et al. 2000), and were captured at sites with higher flow.

Mahmoud (1969) compared the ecology of four species of kinosternid turtles in Oklahoma, but included few comparisons where multiple species were living in sympatry. Three species were sympatric at GEWMA, allowing for a comparison of habitat use when in sympatry. In Oklahoma, Mahmoud (1969) reported capturing Razorback Musk Turtles and Common Musk Turtles together, but they were rarely found with Eastern Mud Turtles. Even though the two species of musk turtles were captured at common sites, Mahmoud (1969) did observe difference in microhabitat use, with Razorback Musk Turtles using deeper water. While sampling the Mountain Fork and Little rivers in

southeastern Oklahoma, Riedle et al. (2009) reported capturing Razorback Musk Turtles at sites with deeper water, faster current, and sandier substrate than at sites where Common Musk Turtles were captured. Eastern Mud Turtles were rarely captured at the same sites as the two musk turtles in either study. Even though all three kinosternids occurred within a small area in this study, they exhibited similar patterns of habitat segregation, with Eastern Mud Turtles found in heavily vegetated marshes, while the two *Sternotherus* species were associated with slightly increased depth and flow. Eastern Mud Turtles are physiologically adapted to the ephemeral nature of their habitat, as they can aestivate during prolonged dry periods (Ernst and Lovich 2009); whereas, both species of musk turtles exhibit high rates of evaporative water loss, restricting terrestrial activity and estivation ability (Stone and Iverson 1999; Constanzo et al. 2001).

Riedle et al. (2009) considered both Common Snapping Turtles and Alligator Snapping Turtles to be ecological generalists based on comparisons of habitat use across several river systems in Oklahoma. When sampled on a smaller geographic scale, these two chelydrids exhibited segregation in habitat use. Generally, Common Snapping Turtles will occupy almost any aquatic habitat, but prefer still or slow moving water with muddy substrates and aquatic vegetation (Bodie et al. 2000; Ernst and Lovich 2009). Alligator Snapping Turtles, on the other hand tend to occupy larger and deeper water bodies (Ewert et al. 2006). Both species are large predators/scavengers and therefore, competition for food resources and predation upon one another may be driving their spatial

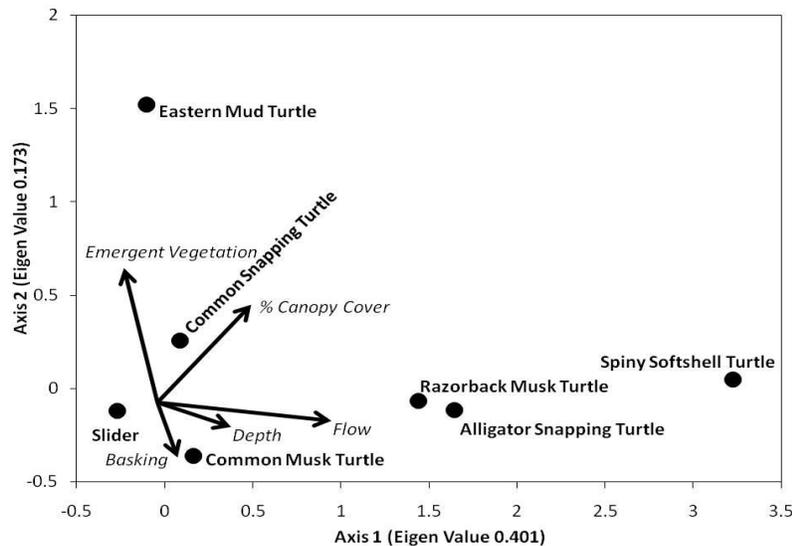


FIGURE 2. Ordination of aquatic turtle species from Gus Engeling Wildlife Management Area, Anderson County, Texas based on Canonical Correspondence Analysis using species abundance and environmental variables (only the first two gradients are shown). Contributions of environmental variables to each gradient are represented by vectors. Total inertia for all axes is 4.983.

distribution when occurring in sympatry (Lescher et al. 2013). Thermoregulation may also promote use of deeper habitats by the larger Alligator Snapping Turtle (Riedle et al. 2006; Fitzgerald and Nelson 2011).

Our analyses supported previous findings that aquatic turtles segregate along gradients associated with flow regimes (Bodie et al. 2000; Anderson et al. 2002; Dreslik and Phillips 2005). Certain species from the regional species pool, primarily map turtles (*Graptemys* spp.), were not captured during our surveys. Stream order may play a role in segregating species across larger spatial scales, particularly for species like map turtles (Fuselier and Edds 1994). Working on a small scale within GEWMA, we were able to elucidate and build upon existing information concerning several species that have not been closely studied where they occur in sympatry with confamilial species. Implementation of similar, intensive, localized sampling across a regional scale would greatly improve our understanding of turtle assemblage patterns across the landscape.

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#### LITERATURE CITED

- Anderson, R.V., M.L. Gutierrez, and M.A. Romana. 2002. Turtle habitat use in a reach of the upper Mississippi River. *Journal of Freshwater Ecology* 17:171–177.
- Bodie, R.J., and R.D. Semlitsch. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia* 122:138–146.
- Bodie, R.J., R.D. Semlitsch, and R.B. Renken. 2000. Diversity and structure of turtle assemblages: associations with wetland characters across a flood plain landscape. *Ecography* 23:444–456.
- Buhlmann, K. A., T.S.B. Akre, J.B. Iverson, D. Karapatakis, R. Mittermeier, A. Georges, A.G.J. Rhodin, P.P. van Dijk, and J.W. Gibbons. 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. *Chelonian Conservation and Biology* 8:116–149.
- Buhlmann K.A., and J.W. Gibbons. 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: implications for wetland conservation boundaries. *Chelonian Conservation and Biology* 4:115–127.
- Cagle, F.R., and A.H. Chaney. 1950. Turtle populations in Louisiana. *The American Midland Naturalist* 43:383–388.
- Costanzo, J.P., J.D. Litzgus, J.B. Iverson, and R.E. Lee, Jr. 2001. Cold-hardiness and evaporative water loss in

- hatchling turtles. *Physiological and Biochemical Zoology* 74:510–519.
- Donner-Wright, D.M., M.A. Bozek, J.R. Probst, and E.M. Anderson. 1999. Responses of turtle assemblage to environmental gradients in the St. Croix River in Minnesota and Wisconsin, USA. *Canadian Journal of Zoology* 77:989–1000.
- Dreslik, M.J., and C.A. Phillips. 2005. Turtle communities in the Upper Midwest, USA. *Journal of Freshwater Ecology* 20:149–164.
- Ernst, C.H., and J.E. Lovich. 2009. *Turtles of the United States and Canada*. The John Hopkins University Press, Baltimore, Maryland, USA.
- Ewert, M.A., D.R. Jackson, D.R., and P.E. Moler. 2006. *Macrochelys temminckii*—Alligator Snapping Turtle. Pp. 58–71 *In* *Biology and Conservation of Florida Turtles*. Chelonian Research Monograph 3. Meylan, P.A. (Ed). Chelonian Research Foundation, Leominster, Massachusetts, USA.
- Fitzgerald, L.A., and R.E. Nelson. 2011. Thermal biology and temperature-based habitat selection in a large aquatic ectotherm, the Alligator Snapping Turtle, *Macrochelys temminckii*. *Journal of Thermal Biology* 36:160–166.
- Fuselier, L., and D. Edds. 1994. Habitat partitioning among three sympatric species of map turtles, genus *Graptemys*. *Journal of Herpetology* 28:154–158.
- Gotelli, N.J., and G.L. Entsminger. 2001. EcoSim: null models software for ecology. Version 7.0. Acquired Intelligence Inc. and Kesity-Bear, Montrose, Colorado, USA.
- Iverson, J.B. 1992. Global correlates of species richness in turtles. *The Herpetological Journal* 2:77–81.
- Klemens, M.W. 2000. *Turtle Conservation*. Smithsonian Institution Press, Washington, DC, USA.
- Koper, N., and R.J. Brooks. 1998. Population size estimators and unequal catchability in Painted Turtles. *Canadian Journal of Zoology* 76:458–465.
- Lemmon, P.E. 1957. A new instrument for measuring forest overstory density. *Journal of Forestry* 55:667–668.
- Lescher, T.C., Z. Tang-Martinez, and J.T. Briggler. 2013. Habitat use by the Alligator Snapping Turtle (*Macrochelys temminckii*) and Eastern Snapping Turtle (*Chelydra serpentina*) in southeastern Missouri. *American Midland Naturalist* 169:86–96.
- Lindeman, P.V. 2000. Resource use of five sympatric turtle species: effects of competition, phylogeny, and morphology. *Canadian Journal of Zoology* 78:992–1008.
- Lindeman, P.V. 2001. Turtle fauna of the upper Tradewater River near Dawson Springs, Kentucky. *Journal of the Kentucky Academy of Science* 62:121–124.
- Lindeman, P.V., and A.F. Scott. 2001. Over three decades of persistence of a small and apparently isolated population of Painted Turtles (*Chrysemys picta*) in a Kentucky reservoir. *Chelonian Conservation and Biology* 4:206–208.
- Losos, J.B. 1996. Phylogenetic perspectives on community ecology. *Ecology* 77:1344–1354.
- Luiselli, L. 2008. Resource partitioning in freshwater turtle communities: a null model meta-analysis of available data. *Acta Oecologica* 34:80–88.
- Mahmoud, I.Y. 1969. Comparative ecology of the kinosternid turtles of Oklahoma. *Southwestern Naturalist* 14:31–66.
- Moll, D., and E.O. Moll. 2004. *The Ecology, Exploitation, and Conservation of River Turtles*. Oxford University Press, New York, New York, USA.
- Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74:2215–2230.
- Pianka, E.R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:737–741.
- Pritchard, P.C.H. 1989. *The Alligator Snapping Turtle: Biology and Conservation*. Milwaukee Public Museum, Milwaukee, Wisconsin, USA.
- Ream, C., and R. Ream. 1966. The influence of sampling methods on the estimation of population structure in Painted Turtles. *American Midland Naturalist* 75:325–338.
- Riedle, J.D. 2014. *Aquatic vertebrate assemblages in the Middle Trinity River Basin with an emphasis on turtles*. Ph.D. Dissertation, Texas A&M University, College Station, Texas, USA. 118 p.
- Riedle, J.D., P.A. Shipman, S.F. Fox, and D.M. Leslie. 2006. Microhabitat use, home range, and movements of the Alligator Snapping Turtle, *Macrochelys temminckii*, in Oklahoma. *Southwestern Naturalist* 51:35–40.
- Riedle, J.D., P.A. Shipman, S.F. Fox, and D.M. Leslie. 2009. Habitat associations of aquatic turtle communities in eastern Oklahoma. *Proceedings of the Oklahoma Academy of Science* 89:19–30.
- Shipman, P.A., D. Edds, and D. Blex. 1994. *Macrochelys temminckii* (Alligator Snapping Turtle) and *Chelydra serpentina* (Common Snapping Turtle): Agonistic behavior. *Herpetological Review* 25:24–25.
- Stephens, P.R., and J.J. Weins. 2003. Explaining species richness from continents to communities: The time for speciation effect in emydid turtles. *American Naturalist* 161:112–128.
- Stephens, P.R., and J.J. Weins. 2004. Convergence, divergence, and homogenization in the ecological structure of emydid turtle communities: The effects of phylogeny and dispersal. *American Naturalist* 164:244–254.
- Stone, P.A., and J.B. Iverson. 1999. Cutaneous surface area in freshwater turtles. *Chelonian Conservation and Biology* 3:512–515.

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ter Braak, C.J.F. 1987. CANOCO – a FORTRAN program for community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis. Version 2.1. ITI-TNO, Wageningen, The Netherlands.

ter Braak, C.J.F., and I.C. Prentice. 1988. A theory of gradient analysis. *Advances in Ecological Research* 18:271–313.

ter Braak, C.J.F., and P.F.M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57:255–289.

Vandewalle, T.J. and J.L. Christiansen. 1996. A relationship between river modification and species richness of freshwater turtles in Iowa. *Journal of the Iowa Academy of Sciences* 103:1–8.



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