

AQUATIC VERTEBRATE ASSEMBLAGES IN THE MIDDLE TRINITY RIVER  
BASIN, WITH EMPHASIS ON TURTLES

A Dissertation

by

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## ABSTRACT

Rivers are dynamic ecosystems with considerable heterogeneity across multiple spatial scales. Environmental factors, such as depth, physical structure, flow regime and habitat connectivity influence species distributions across a floodplain, and subsequently there is a large body of work focused on understanding how these factors influence the structure of fish communities. There has also been increasing interest in understanding how environmental variation influences the community structure of another major aquatic vertebrate group, the turtles. I sampled fish and turtles at Gus Engeling Wildlife Management Area (WMA) and used ordination analyses to visualize environmental gradients that may influence community structure for these two vertebrate groups. Distributions of aquatic turtles and fishes at Gus Engeling WMA were associated with environmental gradients defined by flow regimes and substrate composition. When just turtles were considered, flow regimes were particularly important in describing habitat partitioning among species, particularly confamilial groups. A second study site, Keechi Creek WMA, was sampled for turtles in 2009. Keechi Creek WMA exhibited less habitat heterogeneity than Gus Engeling WMA, and as heterogeneity decreased between the two study sites, turtle species richness decreased, whereas habitat overlap between species increased. I analyzed the capture efficiency of 7 trap types used throughout the course of this project and found that effectiveness of each trap type varied by habitat type, species, and shell size. So, using a diversity of trap types increased my overall trapping success.

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## CHAPTER I

### INTRODUCTION

Stream systems and their associated floodplain habitats are spatially and temporally variable, and as such have proven to be ideal models for studying community assembly, particularly in relation to landscape ecology, and patch dynamics (Grossman *et al.*, 1982; Winemiller *et al.*, 2010). Stream systems, then, may be considered dynamic mosaics of interconnected patches of physical conditions or biological communities (Pringle *et al.*, 1988; Townsend, 1989). Physio-chemical properties of these patches are governed by stochastic events resulting in dynamic and unstable environments (Grossman, 1982). Species abundances are influenced by responses to these unpredictable environmental changes (Sale, 1980), resource partitioning (Schoener, 1974), or predation on competitive dominants (Paine, 1974; 1976).

In a review of current landscape level research on stream habitats and biological assemblages, Hughes *et al.* (2006) discussed the need to improve our understanding of the influences of spatial factors on instream biota. Within that edited volume, the only aquatic taxa discussed were fish and macroinvertebrates. Yet, there is evidence for strong biotic interactions between terrestrial and aquatic biota (Naiman and Rogers, 1997; Naiman *et al.*, 2002). Additionally, changes to riparian habitats can have effects on aquatic habitats, and in turn influence species assemblages of fish (Decamps, 1993; Schlosser, 1995). To address the need to improve our knowledge of stream ecosystems, we must expand our scope of interest to other taxa.

Vellend (2010) defines community ecology as the study of patterns in diversity, abundance, and composition of species in communities, and the processes underlying these patterns. Community ecology as a discipline is considered “messy” as the mechanisms structuring species assemblages are complex and, for some taxa, are poorly understood (Lawton, 1999). Two alternative paradigms have been proposed for the assembly of biological communities. Communities may be strongly influenced by dispersal and assembled randomly (Conner and Simberloff, 1979), or their structure may be non-randomly influenced by biotic interactions, especially competition and predation (Diamond, 1975). There is considerable evidence for both hypotheses. Non-random structure is consistent with processes described by niche theory (Chase and Leibold, 2003; Tilman, 2004). Many observed patterns are consistent with a neutral model of assembly driven by stochastic demographic and dispersal processes (Hubbell, 2001).

Null models describing non-random community structure of fish (Jackson *et al.*, 1992) and turtles (Luiselli, 2008) found that local species assemblages were based on resource dimensions related to micro- and macrohabitat, food, and time. For fish, seasonal fluctuations in water flow, physical and chemical characteristics, available shoreline, sandbars, and islands, and interconnectivity of flowing systems govern local species assemblages in fish (Jackson and Harvey, 1989; Schlosser, 1991; Taylor, 1997). Although less work has been done on turtle communities, previous research has shown strong species segregation between (Anderson *et al.*, 2002; Dreslik and Phillips, 2005) and within (Bodie *et al.*, 2000; Lindeman, 2000) lentic and lotic environments. Within habitats, selection for specific microhabitats by sympatric species of aquatic turtles has

been observed (Cagle, 1942; Fuselier and Edds, 1994; Barko and Briggler, 2006). However, turtle abundances within various habitat patches were found to vary throughout the year depending on water and food availability (Bodie and Semlitsch, 2000; Bodie *et al.*, 2000; Anderson *et al.*, 2002). In general, literature suggests aquatic turtle and fish communities are linked by dispersal of multiple, potentially interacting species. In some sense, aquatic turtles and fish may act as an ecological metacommunity (Leibold *et al.*, 2004) exhibiting similar responses to fluctuations of shared environmental variables.

Although the literature on community assembly of fish and aquatic turtles is considerable, the two taxa have rarely been studied together, although both taxa can be captured using the same gear and methods (Barko *et al.*, 2004). Considering the important roles each taxon plays within aquatic ecosystems, it may be informative to analyze patterns for both groups together, and this could enhance biological assessment programs. Fish assemblages suffer negative effects from physical stressors, such as flow regulation and channel modification, and biological stressors, such as impacts of alien species (Rinne *et al.*, 2005). The same stressors also impact turtles, possibly in a similar manner as fish (Mitchell and Klemens, 2000).

Lawton (1999) and Ricklefs (2008) stress that to truly understand patterns of species assemblage we need to focus on regional scales. The counter point to this argument is that to truly understand process regulating biodiversity ecologists should focus on smaller scales (Brooker *et al.*, 2009). Local-scale processes influence assemblage structures because different species have fitness advantages that depend

upon their abiotic and biotic environment including their own population density (Chesson, 2000). Drivers of local species richness then influence large-scale patterns (Michalet *et al.*, 2002; Urban *et al.*, 2008).

Through the auspices of their Wildlife Diversity Program, the Texas Parks and Wildlife Department focuses on understanding and managing Texas Native species and habitats. Gus Engeling Wildlife Management Area (WMA) in Anderson County, Texas is a 4,434-ha property in eastern Texas consisting of a major tributary of the Trinity River and its associated floodplain (Telfair, 1988). There is considerable interest in managing for the aquatic biodiversity on site (Wes Litterell, TPWD, pers.com.), so I sampled fishes and turtles using the same methods and analyzed patterns of species abundance in relation to physical environmental characteristics (flow, depth, substrate) within different macro-habitat types. My goal was to look for similarity in species assemblages of fishes and turtles among those habitat types, and to examine how abundances of closely related, sympatric species of turtles drives habitat selection.

## CHAPTER II

### HABITAT ASSOCIATIONS OF AQUATIC VERTEBRATES IN AN EAST TEXAS STREAM

#### Introduction

Streams have long been the subject of ecological research that tests hypotheses explaining species assemblage structure, and this is, in part, because standardized sampling methods allow collection of reliable samples of fishes and aquatic macroinvertebrates (Grossman *et al.*, 1982). Knowledge of fish and aquatic macroinvertebrate community ecology has been used to develop biotic indices for determining condition of streams and watersheds (Natural Resources Conservation Service, 2003). Essentially, the structure of communities is treated as a bioassay of stream ecosystems under the assumption that fish and/or macroinvertebrate community patterns should reflect the relative status of ecosystem in response to multiple stressors (Prentice and Cramer, 1990).

A large body of work has been published on the role of abiotic factors in structuring fish assemblages (Matthews and Hill, 1980; Matthews and Styron, 1981; Jackson *et al.*, 2001). These abiotic processes (flow, temperature, nutrient and chemical fluxes) in stream systems are unpredictable, thus, virtually all ecological processes are influenced by spatially and temporally variable biological and physical characteristics of streams (Pringle *et al.*, 1988; Townsend, 1989). Variability in the availability of biotic and abiotic resources requires fish to move between habitats in order to obtain those

resources (Dunning *et al.*, 1992). Habitat complementation refers to the spatial proximity of different nonsubstitutable resources or habitat types required by a particular species (Schlosser, 1995). Examples of nonsubstitutable habitats include spawning vs. feeding habitats, or feeding vs. refugia habitats.

Physical and biotic factors governing fish distributions within stream systems are regulated through deterministic processes related to position along a stream course and fluctuations in stream flow (Gorman and Karr, 1978; Johnson *et al.*, 1995). Stream systems exhibit a longitudinal structure that produces a continuum of morphological and hydrological features from the headwaters to the mouth (River Continuum Concept; Vannote, *et al.*, 1980). Morphological and hydrological features along a river course are determined by geomorphic processes (Montgomery, 1999), and interactions and feedbacks between habitat patches (Poole, 2002). Feedback mechanisms within streams and adjacent aquatic habitats are governed by alternating periods of inundation and separation related to annual or semi-annual flooding. These flood pulses are considered one of the most important hydrological features of stream systems (Flood Pulse Concept; Junk *et al.*, 1989). Flood pulses allow for biotic interchange between streams and their associated floodplain habitats (backwaters, oxbows, marshes) altering both species composition, influx of nutrients, and chemical processes in both lentic and lotic habitats (Junk *et al.*, 1989; Bayley, 1995).

The dynamic nature of streams and resultant habitat heterogeneity supports regional species diversity (Galat *et al.*, 1998; Michener and Haeuber, 1998), and local assemblages are influenced by the periodic connectivity provided by flooding (Galat *et*

*al.*, 1998; Winemiller *et al.*, 2000). The spatial arrangement of flood plain habitats is critical, because many species use different habitats during different life history stages (Welcomme, 1979; Schlosser, 1991; 1995). Species-specific dispersal abilities, and size and position of floodplain habitats are important determinants of the structure of fish assemblages (Taylor, 1997; Taylor and Warren, 2001). Wilkinson and Edds (2001) suggested that biotic processes (foraging, reproduction, ontogenetic habitat shifts) may be more important in explaining variation in fish communities than environmental variables.

Many other species of aquatic vertebrates, such as anurans and salamanders (Wells, 2007), turtles (Bodie *et al.*, 2000; Ernst and Lovich, 2009), and crocodilians (Subalusky *et al.*, 2009), also exhibit differential habitat use based on sex, seasonal behavior, life history stage, and seasonal fluctuations and availability of habitat. Most of those vertebrate taxa may also rely on terrestrial floodplain habitats in addition to aquatic ones for completion of life history stages. But, multiple vertebrate taxa are rarely studied simultaneously when addressing the ecology of riparian habitats. Since community structure may be strongly influenced by dispersal (Conner and Simberloff, 1979), or biotic interactions (Diamond, 1975) or both (Ernest *et al.*, 2008, Velland, 2010), it would be beneficial to study assemblage patterns of different taxa utilizing similar habitats.

Freshwater turtles exhibit relatively high species richness in the southeastern United States (Iverson, 1992; Buhlmann *et al.*, 2009) and often make up a significant fraction of the total biomass in the habitats in which they occur (Iverson, 1982; Congdon *et al.*, 1986). Many freshwater turtle species tend to show preferences for either lentic or



lotic habitats, but not both (Anderson *et al.*, 2002; Dreslik and Phillips, 2005). Species living in sympatry may demonstrate selection for specific microhabitats based on basking structure, canopy cover associated with basking structure, flow, depth, and substrate (Cagle, 1942; Lindeman, 2000; Barko and Briggler, 2006). There is variation in these habitat associations, because flood pulses drive species exchanges between backwater scours, wetlands, and the river channel (Bodie and Semlitsch, 2000; Bodie *et al.*, 2000).

Although fish have been used extensively for bioassessment of aquatic ecosystems, it would be useful to explore the utility of sampling additional vertebrate groups, particularly those that can be sampled effectively with a standard methodology. Turtles can be sampled simultaneously with fishes using the same methods (Barko *et al.*, 2004; Barko and Briggler, 2006), and with this in mind, I sampled both fishes and turtles over three summers at two sites in eastern Texas. My primary goals were to describe species patterns between lentic and lotic habitats, specifically relating species abundance to environmental variables such as flow, depth, substrate, and presence of woody debris.

### Study Area

The Trinity River originates north of the Dallas/Fort Worth metroplex in northeastern Texas, and flows 1150 km southward to empty into Galveston Bay on the Gulf Coast. The Trinity River Basin lies solely within Texas encompassing 46,540 km<sup>2</sup>, and roughly one-third of the state's population (Huser, 2000). Annual rainfall is approximately 100 cm/yr (Johnson, 1931), and the drainage experiences frequent

flooding, particularly within its upper reaches (Huser, 2000). Because there are major urban centers in the Middle Trinity River Basin, the stretch of river between Dallas/Fort Worth and Houston is considered an area of concern by the Texas Parks and Wildlife Department (TPWD; Bill Adams, TPWD, pers. com.). The Middle Trinity River Basin encompasses the Texas Natural Regions of the East Texas Plains and the Prairies Province, and the bisection of moderately humid grasslands and humid cross-timbers habitats by the Trinity River results in high species richness of both flora and fauna (Johnson, 1931).

My study area was located in Anderson County, Texas, on the TPWD managed Gus Engeling Wildlife Management Area (WMA); (Fig. 2.1). Gus Engeling WMA is a 4,434-ha property encompassing a large portion of the Catfish Creek ecosystem. Catfish Creek is a tributary in the Middle Trinity River Basin, encompassing 730 ha and 32 km of Anderson and Henderson counties and considered a Natural National Landmark (Telfair, 1988). Twenty-four small creeks feed Catfish Creek, most of which are spring fed. Habitats associated with the Catfish Creek ecosystem include post-oak (*Quercus stellata*) savanna, bottomland hardwoods, marshes, swamps, bogs, and springs. Aquatic habitat at Gus Engeling WMA is represented by Catfish Creek and its tributaries, adjacent scours and backwater habitat, open canopy marshes, several small ponds and larger lakes. Aquatic habitat is augmented by a series of levees and flood-control gates, built in cooperation with Ducks Unlimited, to provide wetlands for waterfowl. In addition, there are several ponds or “borrow” pits associated with the levees (Wes Litterell, TPWD, pers.com.).

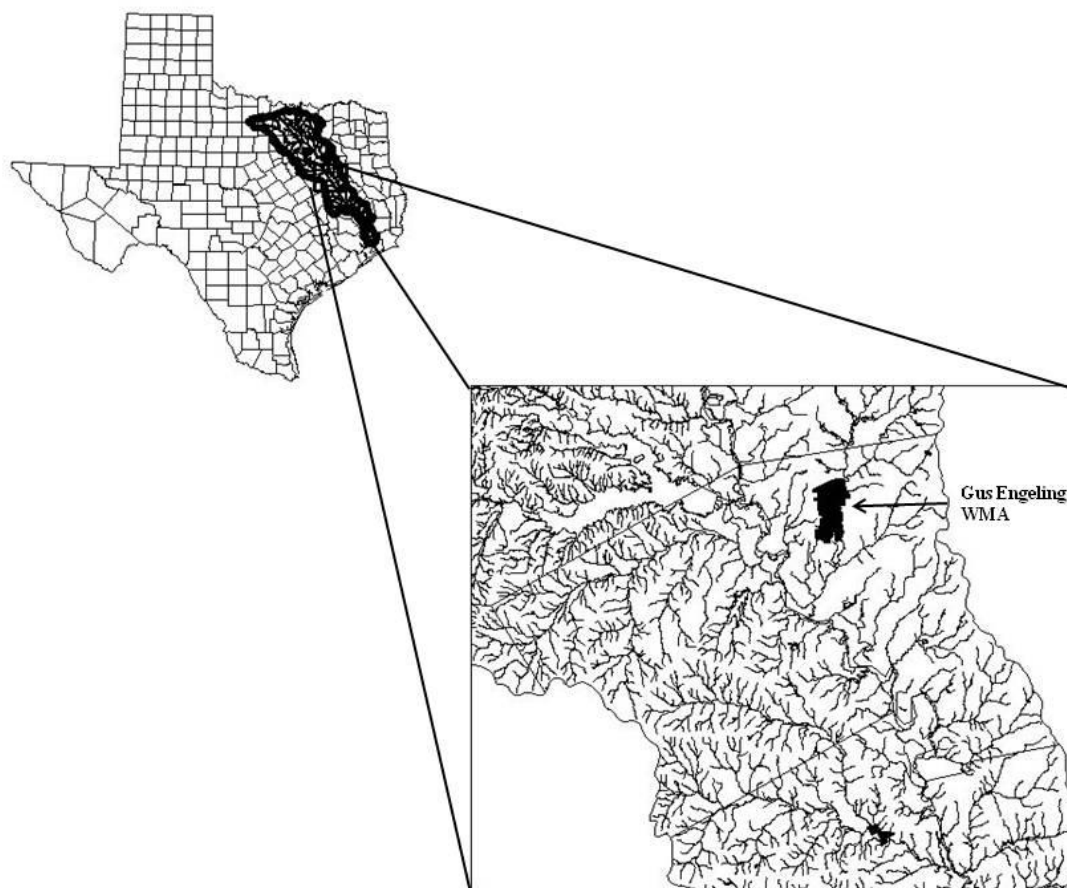


Figure 2.1. The geographic location of the Trinity River Basin in Texas with inset showing the location of Gus Engeling Wildlife Management Area within the Middle Trinity River Basin.

Between the 1860's and 1950's, both upland and bottomland habitats within the Catfish Creek Ecosystem were cleared and burned for livestock grazing. By 1951, livestock was removed within Gus Engeling WMA in order to restore terrestrial habitats (Huser, 2000). Habitat restoration is now augmented through seasonal burns of upland habitat and maintenance of permanent wetlands and seasonal backwater habitats (Wes Litterell, TPWD, pers.com.). The biotic diversity of Gus Engeling WMA prior to European settlement is unknown, but at least 88 fish species, 22 amphibian species, 58 reptilian species, 194 avian species, 45 mammalian species (Telfair, 1988), and over 1,000 plant species (Singhurst *et al.*, 2003) are known to occur on the area.

## Methods

*Sampling.*—I sampled aquatic habitats at Gus Engeling WMA using a variety of trap gear between late May and late July, 2006-2008 and between April and late July 2009. During each sampling period I set one large and small fyke net, 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; [www.christensennetworks.com](http://www.christensennetworks.com)) was 4.5 m in length (front frame to cod end) with a single 14.5 m x 88 cm lead. The two anterior rectangular frames were 120 cm x 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; [www.christensennetworks.com](http://www.christensennetworks.com)) was 3.3 m in length from the front frame to cod end, and had a single 7.4 m x 67 cm lead. The two rectangular front frames were 95 cm x 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. Square mesh size was 1cm. The larger hoop (turtle net; Memphis Net and Twine; [www.memphisnet.net](http://www.memphisnet.net)) consisted of three 88-cm diameter metal rings and one 31-cm diameter stretchable funnel. Overall trap length was 245 cm, and square mesh size was 2.5 cm.

The collapsible box traps and sea bass traps were purchased from Memphis Net and Twine ([www.memphisnet.net](http://www.memphisnet.net)). 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 was 2.5cm. Small box traps were 59 cm x 43 cm x 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 x 60 cm x 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 x 64 cm x 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.

All traps were baited with sardines and/or fresh fish. Traps were checked at least once every 24hrs, 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. Aquatic habitats at Gus Engeling WMA were highly variable in size, based on seasonal and annual rainfall. The type and number of traps set was dictated by the

amount of water available, depth of available water, and number of nets available at that time.

*Data Collection.*—All turtles and fishes captured were identified to species and enumerated. To address abiotic factors driving community composition of aquatic turtles and fishes, I measured structural and chemical variables using methodology similar to that collected for fishes (Edds, 1993) and turtles (Fuselier and Edds, 1994) at each trap. Structural data included canopy cover, depth, flow, basking availability, substrate composition, and emergent vegetation. Canopy cover was recorded at the trap using a concave forestry densitometer (Lemmon, 1957). Depth was recorded at the opening of the trap gear. Flow was also recorded at the opening of the trap gear using a handheld flow meter averaging current speed at 5 points within the water column. Basking site availability was recorded as the percentage of exposed surface (bank, emergent woody debris) present within a 25-m diameter area surrounding the trap. Emergent vegetation was recorded as the percentage of aquatic vegetation present within a 25-m diameter area surrounding each trap. Substrate composition was divided into percent sand, mud, clay and detritus and was recorded within a 25-m diameter area surrounding each trap. Clay was defined as a sticky-fined grained soil type that was either yellow or bluish gray in color at this site. Sand was a looser, large granular substrate. Mud was defined as soft, sticky earthy matter that did not fit into the clay or sand substrate types. Detritus was defined as dead and decaying vegetative matter (leaves, woody debris).

Physico-chemical data included water temperature, dissolved oxygen (DO), and PH. Water temperature was recorded by placing a thermometer on the substrate roughly

0.5 m from the shore. Dissolved oxygen was determined using a Winkler Titration Kit (LaMotte, Chestertown, MA). I determined PH using a Colorimetric Octet Comparator kit (LaMotte, Chestertown, MA).

I classified habitat according to five types: Creek (flowing waters associated with Catfish Creek and its tributaries); Backwater (scours and flooded timber associated with the Catfish Creek floodplain); Marsh (shallow, open 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 and consisting of more open water than marshes); and Lakes (larger, several ha manmade water bodies).

*Data analysis.* —I used the PROC GLM procedure for mean comparisons in SAS (SAS Institute, Inc., Cary, NC, 1989) to compare microhabitat variables collected at each site (net) amongst five habitat types identified at Gus Engeling WMA. The PROC GLM procedure relates continuous dependent variables to independent variables. The independent variables act as classification variables, which divide observation into distinct groups, in this case, macrohabitats. I calculated number of captures per net night (1 net set for 1 night = 1 net night) by habitat type for fish and turtles to identify species associations amongst different habitats.

To address relationships between fish, turtles, and measured environmental variables collected at common sites (traps), I compared species distributions for turtles using ordination analyses. I used a direct ordination method, canonical correspondence analysis (CCA, Palmer, 1993; ter Braak and Verdonschot, 1995), to fit species patterns to environmental variables. CCA 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 the independent variables (Palmer, 1993). Essentially, CCA allows one to examine the effect of environmental variables on community patterns (Palmer, 1993; ter Braak and Verdonschot, 1995). One can then compare the variance of the turtle data that is explained by the ordination axes derived by fish in co-correspondence analysis with those derived by environmental variables in canonical correspondence analysis (ter Braak and Schaffers, 2004). All CCA's were run using CANACO version 4.5 (ter Braak, 1987) and Monte Carlo Permutation tests were run in conjunction with the CCA to determine which environmental variables were important in describing fish and turtle distributions.

## Results

Total sampling effort at Gus Engeling WMA between 2007-09 was 1,088 net-nights (2007 = 222 net nights; 2008 = 372 net nights; 2009 = 494 net nights). I set 210 net nights in creek habitat, 521 net nights in backwater habitat, 160 net nights in marsh habitat, 139 net nights in pond habitat, and 58 net nights in lake habitat. The amount of water in each habitat, and thus the amount of habitat available in which to set nets, was highly variable depending on recent precipitation events.

I captured 366 turtles of eight species and 2,935 fishes of 31 species (Table 2.1). River cooters (*Pseudemys concinna*) were never captured using sampling gear, even though many river cooters were observed at several sites. Thus, I excluded river cooters



from the ordination analyses. Only fish species with  $\geq 10$  captures were used in the analyses (Table 2.2).

Table 2.1: Complete species list of aquatic turtles and fishes captured at Gus Engeling WMA, Anderson County, Texas, 2007-2009.

Common Name	Scientific Name
Common Snapping Turtle	<i>Chelydra serpentina</i>
Alligator Snapping Turtle	<i>Macrochelys temminckii</i>
Eastern Mud Turtle	<i>Kinosternon subrubrum</i>
Common Musk Turtle	<i>Sternotherus odoratus</i>
Razorback Musk Turtle	<i>Sternotherus carinatus</i>
Spiny Softshell Turtle	<i>Apalone spinifera</i>
River Cooter	<i>Pseudemys concinna</i>
Slider	<i>Trachemys scripta</i>
Alligator Gar	<i>Atractosteus spatula</i>
Spotted Gar	<i>Lepisosteus oculatus</i>
Bowfin	<i>Amia calva</i>
Gizzard Shad	<i>Dorosoma cepedianum</i>
Threadfin Shad	<i>Dorosoma petenense</i>
Blacktail Shiner	<i>Cyprinella venusta</i>
Golden Shiner	<i>Notemigonus crysoleucas</i>
Western Starhead Topminnow	<i>Fundulus blairae</i>
Lake Chubsucker	<i>Erimyzon sucetta</i>
Smallmouth Buffalo	<i>Ictiobus bubalus</i>
Spotted Sucker	<i>Minytrema melanops</i>
Black Bullhead	<i>Ameiurus melas</i>
Yellow Bullhead	<i>Ameiurus natalis</i>
Channel Catfish	<i>Ictalurus punctatus</i>

Table 2.1 cont.

Common Name	Scientific Name
Tadpole Madtom	<i>Noturus gyrinus</i>
Freckled Madtom	<i>Noturus nocturnus</i>
Grass Pickerel	<i>Esox americanus</i>
Pirate perch	<i>Aphredoderus sayanus</i>
Flier	<i>Centrarchus macropterus</i>
Green Sunfish	<i>Lepomis cyanellus</i>
Warmouth	<i>Lepomis gulosus</i>
Orangespotted Sunfish	<i>Lepomis humilis</i>
Bluegill	<i>Lepomis macrochirus</i>
Dollar Sunfish	<i>Lepomis marginatus</i>
Longear Sunfish	<i>Lepomis megalotis</i>
Redear Sunfish	<i>Lepomis microlophus</i>
Spotted Sunfish	<i>Lepomis punctatus</i>
Bantam Sunfish	<i>Lepomis symmetricus</i>
Black Bass	<i>Micropterus</i> sp.
White crappie	<i>Pomoxis annularis</i>
Black Crappie	<i>Pomoxis nigromaculatus</i>

Table 2.2: Catch per unit effort by habitat type for species used in community analyses at Gus Engeling Wildlife Management Area, Anderson County, Texas, 2007-2009.

Species	Total Captures	Catch/Unit Effort by Habitat Type				
		Creek	Backwater	Marsh	Pond	Lake
Redear Slider	264	0.05	0.34	0.18	0.60	1.07
Razorback Musk Turtle	25	.12	0.03	0	0	0
Common Musk Turtle	18	0.03	0.02	<0.01	<0.01	0
Common Snapping Turtle	17	<0.01	0.04	0.01	0.05	0
Eastern Mud Turtle	24	0	<0.01	0.10	0	0
Alligator Snapping Turtle	12	0.04	<0.01	0	0	0.01
Spiny Softshell Turtle	7	0.03	<0.01	<0.01	<0.01	0
Bluegill	895	0.55	0.52	0.28	0.77	6.96
Flier	481	0.02	0.80	0.18	0.24	0
Yellow Bullhead	316	0.66	0.16	0.47	0.02	0.30
Black Bullhead	280	0.23	0.14	0.15	0.24	0.31
Warmouth	245	0.10	0.35	0.07	0.08	0.22
Black Crappie	233	0.20	0.27	0.20	0.11	0
Redear Sunfish	133	<0.01	0.02	0.01	0.03	1.88
Longear Sunfish	44	0.19	<0.01	<0.01	0	0
Dollar Sunfish	33	0	0.06	0.01	<0.01	0
Spotted Gar	27	0.10	0.01	0	0	0
Bowfin	26	<0.01	0.03	0.03	0.03	0
Green Sunfish	26	0.06	<0.01	0.07	0	0
Spotted Sunfish	26	0.07	0.01	<0.01	0	0
Alligator Gar	25	0.08	0.01	0	0	0
Gizzard Shad	20	<0.01	0.03	0	0	0
Grass Pickerel	20	0.02	0.02	0.03	0	0
Lake Chubsucker	16	0.02	0	0.08	0	0.05
Pirate Perch	16	0	0.03	<0.01	0	0
Golden Shiner	15	<0.01	0.02	<0.01	0	0
White Crappie	9	0.02	0.01	0	0	0
Smallmouth Buffalo	8	0.04	<0.01	0	0	0
Orangespotted Sunfish	8	0.03	<0.01	0.01	0	0
Bantam Sunfish	8	<0.01	<0.01	0.02	0	0
Spotted Sucker	6	0.01	<0.01	0	0	0

Characteristics of each habitat type based on environmental variables collected at each site (net) differed based on substrate, canopy cover, depth, and flow (Table 2.3). Not surprisingly, creek habitats were deep, had high flow rates, dense canopy cover, moderate to high DO, and predominantly sandy substrate. Backwater habitats tended to be shallow, turbid, and had little to no flow, low DO, moderate canopy cover and substrate that was predominantly mud and sand. Marsh habitats were characterized by shallow water, low DO, sparse canopy cover, dense emergent vegetation, and the substrate was predominantly detritus. Pond habitats had low turbidity, low canopy cover, high PH, high water temperature, and sand and clay substrates. Lakes were characterized by deep water, low turbidity, sparse canopy cover, high DO, moderate presence of emergent vegetation, and a mixed substrate of sand, mud, and detritus.

Canonical correspondence analysis for fish and turtles revealed that flow, substrate, and emergent vegetation were associated with species distributions for fish and turtles (Table 2.4; Fig. 2.2). Substrate composition itself was correlated with flow (higher percentages of sand and clay at sites with higher flow), and emergent vegetation (increasing percentages of detritus at sites with low flow and increasing emergent vegetation). Based on Monte Carlo permutation tests, the presence of basking structure and water temperature also had strong influences on species' distributions. Basking structure was generally represented by downed woody debris, and correlated to increased canopy cover and increased detritus. Water temperature was positively associated with sites that had a more open canopy. The percent variance of the species-environmental relationship for the first two axes of the canonical correspondence

Table 2.3: Mean ( $\pm$  SD) environmental variables measured at each net, by habitat, at Gus Engeling Wildlife Management Area, Anderson County, Texas 2007-2009. Within a row means followed by the same letter are not different  $\alpha = 0.05$ .

Variable	Backwater	Creek	Marsh	Lake	Pond	<i>P</i>
Depth (cm)	36.53 $\pm$ 26.07 a	64.06 $\pm$ 27.09 b	36.19 $\pm$ 26.42 a	49.09 $\pm$ 44.12 e	46.72 $\pm$ 27.43 e	<0.001
Turbidity (cm)	19.45 $\pm$ 8.85 a	28.80 $\pm$ 10.46 b	24.22 $\pm$ 13.76 c	34.09 $\pm$ 24.05 d	33.63 $\pm$ 26.85 d	<0.001
Flow (m/s)	0.06 $\pm$ 0.97 a	0.96 $\pm$ 1.28 b	0.00 $\pm$ 0.00 a	0.01 $\pm$ 0.13 a	0.00 $\pm$ 0.00 a	<0.001
% Canopy Cover	66.84 $\pm$ 39.11 a	90.67 $\pm$ 21.92 b	21.05 $\pm$ 34.51 c	10.54 $\pm$ 22.82 c	29.71 $\pm$ 36.57 d	<0.001
PH	5.95 $\pm$ 2.79 a	6.00 $\pm$ 1.11 a	5.73 $\pm$ 1.54 a	6.39 $\pm$ 0.49 ab	6.95 $\pm$ 4.56 b	<0.001
Dissolved Oxygen (ppm)	3.34 $\pm$ 3.25 a	5.19 $\pm$ 1.77 b	2.61 $\pm$ 2.39 c	7.29 $\pm$ 0.51 d	5.92 $\pm$ 2.52 e	<0.001
Water Temperature	22.79 $\pm$ 7.98 a	24.26 $\pm$ 4.89 b	23.93 $\pm$ 7.15 abc	25.64 $\pm$ 9.4 bcd	27.19 $\pm$ 1.85 d	<0.001
% Sand Substrate	15.25 $\pm$ 15.75 a	44.42 $\pm$ 23.46 b	14.82 $\pm$ 22.78 a	34.00 $\pm$ 21.28 c	31.18 $\pm$ 27.97 c	<0.001
% Mud Substrate	35.54 $\pm$ 18.91 a	28.22 $\pm$ 18.02 b	24.58 $\pm$ 16.89 b	23.09 $\pm$ 10.99 bc	19.89 $\pm$ 22.17 c	<0.001
% Clay Substrate	12.45 $\pm$ 15.50 a	6.17 $\pm$ 11.33 b	15.47 $\pm$ 18.62 ac	17.09 $\pm$ 17.57 ac	30.79 $\pm$ 34.75 d	<0.001
% Detritus Substrate	33.36 $\pm$ 15.15 a	21.65 $\pm$ 22.43 b	41.65 $\pm$ 22.03 c	14.91 $\pm$ 7.61 d	13.99 $\pm$ 10.36 d	<0.001
% Basking Availability	14.36 $\pm$ 16.58 a	15.99 $\pm$ 1.03 ab	1.40 $\pm$ 6.17 c	8.72 $\pm$ 12.25 d	18.16 $\pm$ 17.04 b	<0.001
% Emergent Vegetation	7.74 $\pm$ 18.24 a	5.46 $\pm$ 17.67 a	79.49 $\pm$ 29.26 b	31.05 $\pm$ 30.45 c	26.42 $\pm$ 38.96 c	<0.001

Table 2.4: Species coordinates for Canonical correspondence analysis of fish and turtles at Gus Engeling Wildlife Management Area, Anderson County, Texas 2007-2009.

Turtle Species	Axis 1	Axis 2	Axis 3	Axis 4
Spiny Softshell	0.674	1.253	0.671	-0.001
Common Snapping Turtle	0.163	1.007	-1.011	-0.047
Eastern Mud Turtle	-0.903	1.551	-1.283	1.041
Alligator Snapping Turtle	0.399	1.042	0.332	0.277
Razorback Musk Turtle	0.141	0.901	0.322	0.002
Common Musk Turtle	-0.203	-0.082	0.459	-0.195
Slider	-0.001	0.584	-0.881	-0.064
Alligator Gar	0.252	0.417	0.565	-0.109
Spotted Gar	0.440	0.814	0.583	-0.082
Bowfin	-0.558	0.699	-0.723	0.045
Gizzard Shad	-0.522	0.699	0.697	-0.812
Golden Shiner	-0.262	-0.441	0.351	-0.610
Lake Chubsucker	-0.036	0.629	-0.02	1.909
Smallmouth Buffalo	0.526	-0.252	1.343	-0.346
Spotted Sucker	-0.285	0.735	0.221	0.227
Black Bullhead	-0.360	0.183	-0.329	-0.544
Yellow Bullhead	-0.111	0.395	0.077	0.033
Grass Pickerel	-0.549	0.599	-0.224	0.236
Pirate Perch	-0.422	-0.106	0.149	-0.233
Flier	-0.777	-0.494	0.229	0.259
Green Sunfish	0.207	1.129	-1.341	0.254
Warmouth	-0.337	0.037	-0.090	-0.266
Orange-Spotted Sunfish	0.747	0.633	-0.938	-0.200
Bluegill	0.527	-0.259	0.119	0.169
Dollar Sunfish	-0.326	-0.380	0.610	-0.298
Longear Sunfish	0.566	0.539	1.005	-0.412
Redear Sunfish	1.046	-0.326	0.040	-0.324
Spotted Sunfish	-0.311	0.279	0.196	1.88
White Crappie	-0.499	-0.383	0.719	0.421
Black Crappie	-0.011	-0.249	0.382	-0.320

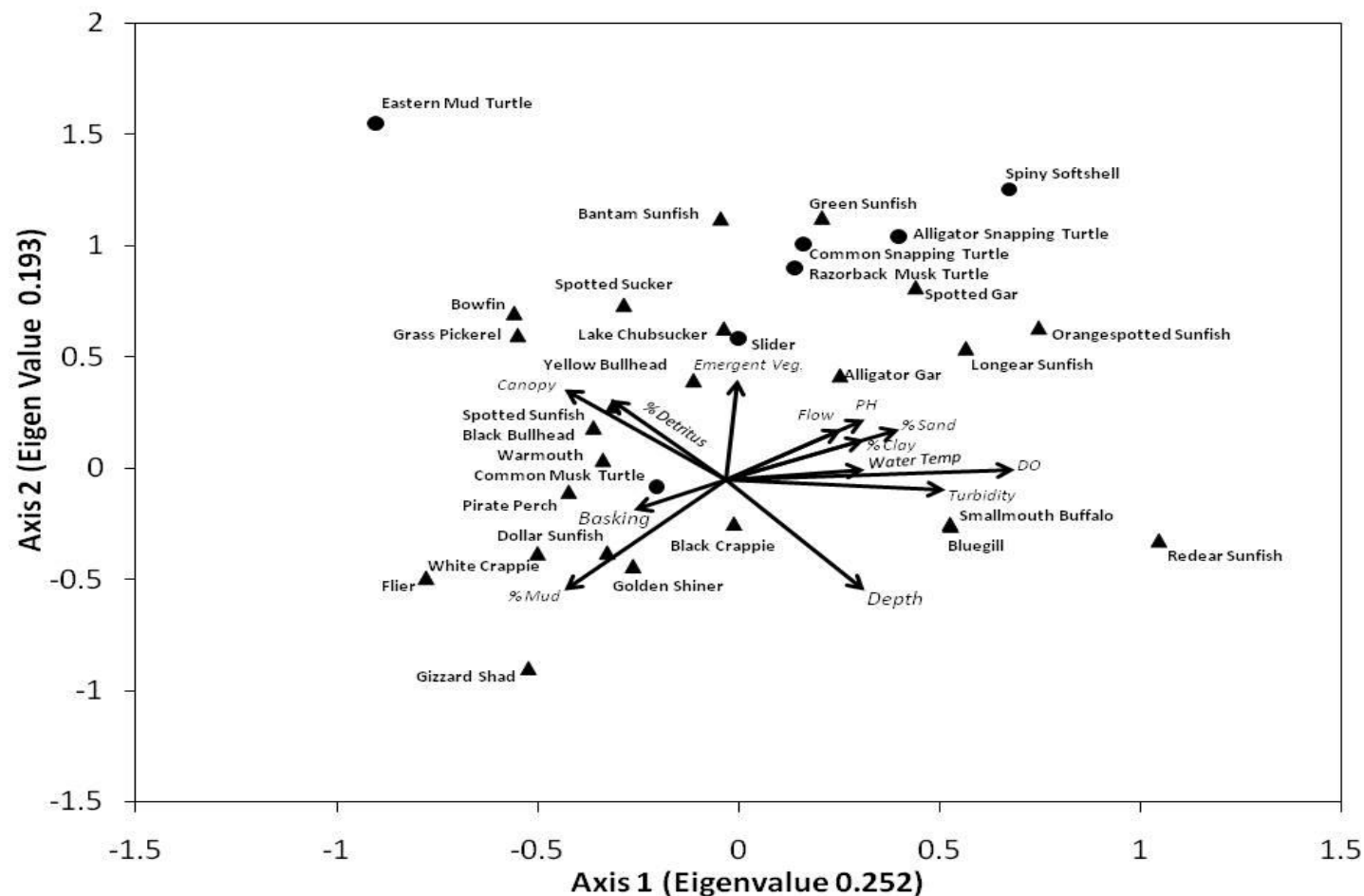


Figure 2.2. Distribution of species scores of turtles, fishes, and environmental variables based on the first and second axes from Canonical correspondence analysis at Gus Engeling Wildlife Management Area. Turtle species scores are represented by circles and fish species scores by triangles. Continuous environmental variables are represented by vectors. Vector representation of turbidity is inverse, with increasing water clarity with increasing distance from the origin. Total inertia for all axes is 12.22.

analysis was 42.7%, while the third and fourth axes explained an additional 27% of the variance.

Scores for spotted gar and spiny softshell turtles within the canonical correspondence analysis were associated with sites with clear water, high flow, high DO, and high percent of sandy substrate (Fig. 2.2). Bowfin, grass pickerel (*Esox americanus*), and spotted suckers (*Minytrema melanops*) were not clearly associated with specific environmental variables. Within the ordination analyses all three species occurred along gradients associated with marsh habitats. However, captures were evenly distributed in backwater and marsh habitat for bowfin and grass pickerel, but creek and backwater habitat had higher captures of spotted suckers.

Bluegill sunfish, redear sunfish, and smallmouth buffalo (*Ictiobus bubalus*) had scores on the first two canonical gradients (Fig 2.2). All three species were associated with sites characterized by greater water depth, and increasing water clarity and dissolved oxygen. Bluegill sunfish were captured most frequently in lake and backwater habitats, redear sunfish in lake habitats, and smallmouth buffalo in creek habitats (Table 2.2). Whereas each species used different macrohabitats, their CCA axis scores suggest that each species used similar microhabitats within their respective macrohabitat type.

## Discussion

One hundred percent of the turtle species and 74% of the fish species I captured at Gus Engeling WMA were captured within the scours and adjacent backwaters (Table 2.2). The presence of aquatic turtles and fish in Catfish Creek and its associated



floodplain appear to be related to annual and seasonal fluctuations in available habitat. The presence of backwater, and to a certain extent marsh, habitats at Gus Engeling WMA are dependent on flood pulses related to seasonal rainfall.

However, not all fish and turtle species were associated with Catfish Creek or its scours. Exceptions included bluegill and redear sunfish, two common centrarchid fishes that are regularly stocked in ponds and lakes (Robison and Buchanan, 1988); (Table 2.2). Compared to other turtles, the eastern mud turtle generally was captured at relatively ephemeral sites. Juvenile bowfins were generally captured at sites along the edges of backwater scours characterized by shallow water and low DO. Eastern mud turtles are relatively terrestrial compared to other aquatic turtles, and also have the ability to estivate (Ernst and Lovich, 2009), and the bowfin is a primitive air breathing fish (Johansen *et al.*, 1970). These physiological adaptations to ephemeral habitats may explain why correspondence analysis grouped these two species grouped together.

The distribution of both aquatic turtles and fishes at Gus Engeling WMA were associated with environmental gradients related to flow and substrate regimes with predictable groupings of both taxa related to specific microhabitat characteristics. Flow, substrate, and emergent vegetation were variables particularly important in determining species distributions. Results from Monte Carlo permutation tests suggested that downed woody debris was a major determining factor in species distributions. Riparian areas, the sources of woody debris, act to regulate the thermal profile of aquatic habitats by shading all or parts of a stream or water body (Welty *et al.*, 2002). Woody debris within stream channels introduces organic matter and nutrients, maintains physical habitat by

decreasing bank incision, decreases sediment flux, and controls pool spacing and bar formation (Abbe and Montgomery, 1996; Brooks *et al.*, 2004). Subsequently, the introduction of woody debris into an aquatic environment results in increase of productivity and diversity of fish and invertebrates (Meffe and Sheldon, 1988; Robertson and Crook, 1999).

Fishes use submerged woody debris as overhead cover from predation, and visual isolation between individuals (Robertson and Crook, 1999). Fishes may also receive a secondary benefit in the form of food from an increase in abundance and richness of aquatic invertebrates associated with woody debris (Angermeier and Karr, 1984; Everett and Ruiz, 1993). Woody debris is important to turtles for aerial basking and refugia (Chaney and Smith, 1950) and as foraging sites (Moll, 1976; Gibbons and Lovich, 1990). Presence of woody debris dictated the distribution of basking species (*Chrysemys*, *Graptemys*, *Pseudemys*, and *Trachemys*); (Lovich, 1988; Lindeman, 1999) as well as bottom dwellers such as *Macrochelys* that depend on submerged woody debris for cover (Riedle *et al.*, 2006; Shipman and Riedle, 2008).

In addition to meeting the energy requirements for aquatic vertebrates, habitat complexity within stream systems allows fishes to meet their life history requirements providing important spawning and nursery habitats (Schlosser, 1991; Schlosser, 1995; Fuasch *et al.*, 2002.). Bowfin and alligator gar (*Atractosteus spatula*) are medium to large fishes, but most of my captures at GEWMA were represented by small juveniles in shallow, heavily vegetated habitats, similar to findings by Etnier and Starnes (1993) and Echelle and Riggs (1972). Although the ecology of hatchling and juvenile life stages of

turtles is poorly studied, it is clear that most turtle species undergo ontogenetic habitat shifts. Clark and Gibbons (1969) found shifts in habitat use and diet in sliders, and Bass (2007) found that hatchling alligator snapping turtles preferred shallower water, with more woody debris and floating vegetation mats when compared with adults. Although total captures were extremely low, hatchling sliders and alligator snapping turtles were captured in shallow, heavily vegetated bodies of water, habitat similar to that described by Clark and Gibbons (1969) and Bass (2007).

Interactions among and between life stages of fishes and turtles at Gus Engeling WMA require additional study in order to begin unraveling the complex interactions between these groups. Expansion of ordination analyses to additional sites within the Middle Trinity River Ecosystem could help to determine how scale and stream order affect the structure of these aquatic vertebrate assemblages over larger gradients. Biodiversity is affected by changes in physical and biological characteristics of landscapes, including movement of individual organisms (Pressey *et al.*, 2007), and therefore understanding the life history needs of all aquatic organisms is essential for management of wetland and riparian corridors (Galat *et al.*, 1998; Bodie *et al.*, 2000; Semlitsch and Bodie, 2003). Results from this study suggest that turtles and fish can be surveyed and considered simultaneously to guide wetland management.

## CHAPTER III

### ECOLOGY OF TWO EASTERN TEXAS AQUATIC TURTLE COMMUNITIES

#### Introduction

Two questions within community ecology are “what are the origins of diversity at a site?” and “how is that diversity maintained?” (McGowan and Walker, 1993; Ricklefs and Schluter, 1993)? It is thought that biogeographic history drives regional species assemblage patterns, whereas environmental conditions and species interactions influence local species compositions (Ricklefs, 1987; Jackson and Harvey, 1989). Species interactions may be explained by either stochastic demographic and dispersal processes (Hubbell, 2001) or by niche theory and competition (Chase and Leibold, 2003; Tilman, 2004). Some have argued it may be a combination of all these processes. Climate, habitat, and resource availability change over time, so there are subsequent shifts in species assemblages because of species-specific niche requirements and dispersal abilities (Ernst *et al.*, 2008).

Ecologists are currently working to better understand how factors, such as 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, habitat 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 (Ernst and Lovich, 2009), 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, adaptive evolution 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 is integral in developing conservation strategies for species and ecosystems. For many taxa, such as turtles, that have undergone worldwide declines (Klemens, 2000), local and regional patterns of community structure are poorly understood.

The Chelonia, as a whole, are experiencing a multitude of anthropogenic stressors, ranging from over-exploitation for trade, habitat loss, and pollution, so many

species are in peril of extinction (Klemens, 2000; Moll and Moll, 2004). In response, turtles are the focus of major conservation efforts (e.g. Turtle Survival Alliance, and the IUCN Tortoise and Freshwater Turtle Specialist Group), but studies of turtle communities are few, and descriptions of life histories for many species are lacking. Despite much concern over the conservation status of turtles, there are relatively few and only very recent descriptions of turtle communities, and how these natural assemblages may be structured.

Luiselli (2008) tested for non-random patterns in turtle community structure using null models based on turtle community data available in peer-reviewed literature. His results suggested that community structure was non-random, and 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).

While most previous research focused either on microhabitat dimensions of turtle community structure or macroecological patterns, little work has been done testing for evidence of intra- and inter-specific competition. Lindeman (2000) found no competition for basking sites among five species (false map turtle [*Graptemys pseudogeographica*],

Ouachita map turtle [*G. ouachitensis*], river cooter [*Pseudemys concinna*], slider, and smooth softshell [*Apalone mutica*) of aquatic turtles, although there were familial splits with Emydids utilizing downed woody debris and Trionychids utilizing bank habitat for basking. Lovich (1988) noted intraspecific competition for basking sites among individuals of painted turtles (*Chrysemys picta*). Basking structure may be a limiting factor in determining density and richness in *Graptemys* (Lindeman, 1999) not only for thermoregulation (Cagle, 1950) but also for shelter and forage (Everett and Ruiz, 1993). Work on dietary overlap is also scarce, but two studies found a decrease in dietary similarity with increasing densities in neotropical turtle communities (Vogt and Guzman-Guzman, 1988; Moll, 1990).

To better understand how local scale processes influence the structure of turtle communities, I sampled a site in east Texas in 2006-2008 to 1) test for segregation of turtle species along measured environmental gradients, and 2) determine degree of overlap of use of macrohabitats. In 2009, I sampled a second site within the same river drainage with the objectives to compare 1) species richness and similarity of community structure between sites, 2) differences in habitat use among species between sites, and 3) population structure (size and sex ratios) between sites.

### Study Area

My primary study area was located in Anderson County, Texas, on the Texas Parks and Wildlife Department (TPWD) managed Gus Engeling Wildlife Management Area (WMA); (Fig. 3.1). Gus Engeling WMA is a 4,434-ha property encompassing a

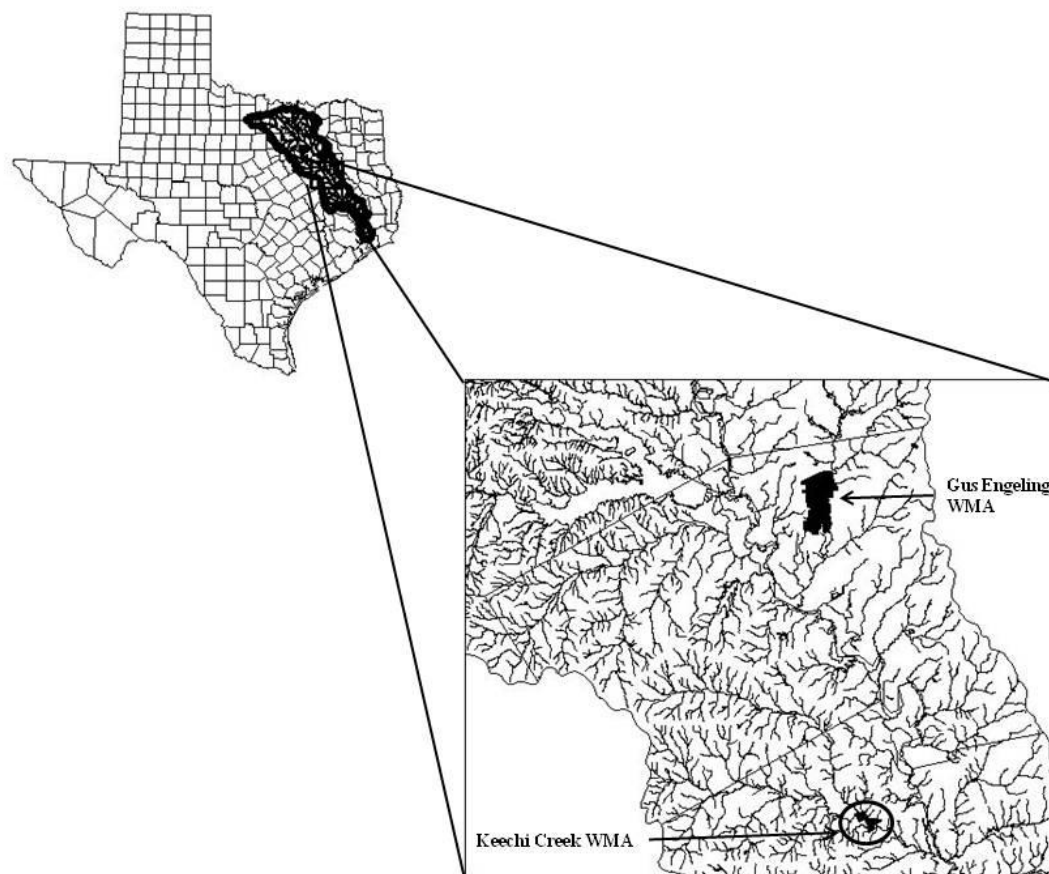


Figure 3.1. The geographic location of the Trinity River Basin in Texas with inset showing the location of Gus Engeling and Keechi Creek WMA's.



large portion of the Catfish Creek ecosystem. Twenty-four small creeks feed Catfish Creek, most of which are spring fed. Habitats associated with the Catfish Creek ecosystem include post-oak (*Quercus stellata*) savanna, bottomland hardwoods, marshes, swamps, bogs, and springs. Aquatic habitat at Gus Engeling WMA is represented by Catfish Creek and its tributaries, adjacent scours and backwater habitat, open canopy marshes, several small ponds and larger lakes. Aquatic habitat is augmented by a series of levees and flood-control gates, built in cooperation with Ducks Unlimited, to provide wetlands for waterfowl. In addition, there are several ponds or “borrow” pits associated with the levees (E. Wolverton, TPWD pers. comm.).

My second site was the TPWD managed Keechi Creek WMA in northeastern Leon County, Texas. Keechi Creek WMA, a small 607 ha management area, also lies within the Middle Trinity River Basin and was acquired by TPWD in 1986 (Fig. 3.1). Aquatic habitats at Keechi Creek WMA are much less complex, consisting of Keechi and Buffalo creeks, and a large oxbow lake associated with Keechi Creek. The oxbow lake is intermittently connected to both creeks (Gelwick *et al.*, 2001). Terrestrial habitat is predominately bottomland hardwoods. Hardwoods in this region are typified by green ash (*Fraxinus pennsylvanica*), boxelder (*Acer negundo*), bur oak (*Quercus macrocarpa*), Shumard oak (*Q. shumardii*), overcup oak (*Q. lyrata*), water oak (*Q. nigra*), willow oak, (*Q. phellos*) and post oak (*Q. stellata*); (Ryberg *et al.* 2004).

Little work has been done describing the terrestrial vertebrate communities on Keechi Creek WMA. In 1999 a baseline inventory of vertebrates was undertaken by

Texas A&M University (L. Fitzgerald, pers. comm.). The survey resulted in the capture of 11 species of amphibians, 16 species of reptiles, and 13 species of mammals. The fish community has been described more extensively, and is composed of at least 34 species (Gelwick *et al.*, 2001).

Potential mammalian predators of turtle nests or adults in this region include eastern spotted skunks (*Spilogale putorius*), striped skunk (*Mephitis mephitis*), raccoons (*Procyon lotor*), feral hogs (*Sus scrofa*) and armadillos (*Dasypus novemcinctus*) via rooting in the soil near nests (Schmidly, 1983). Raccoons in particular are major predators of turtle nests and hatchlings (Ernst and Lovich, 2009). Raccoon densities appear to be increasing across their range because of decreases in pelt prices and increasing subsidization by humans (Gehrt *et al.*, 2002; Landholt and Genoways, 2002).

There are differences in natural and anthropomorphic perturbations between Gus Engeling and Keechi Creek WMAs. Gus Engeling WMA had additional perturbations acting upon adult turtles, which are not present at Keechi Creek WMA. These impacts include predation pressure by alligators (*Alligator mississippiensis*) and human related activity such as increased road density and high density of set lines (limb lines, trot lines) for fishing. The American alligator is common at Gus Engeling WMA, but rare to nonexistent at Keechi Creek WMA.

## Methods

*Sampling.*—I sampled aquatic habitats at Gus Engeling WMA using a variety of trap gear between mid-April and late July, 2006-2008 and between April and late July

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; [www.christensennetworks.com](http://www.christensennetworks.com)) was 4.5 m in length (front frame to cod end) with a single 14.5 m x 88 cm lead. The two anterior rectangular frames were 120 cm x 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; [www.christensennetworks.com](http://www.christensennetworks.com)) was 3.3 m in length from the front frame to cod end, and had a single 7.4 m x 67 cm lead. The two rectangular front frames were 95 cm x 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. Square mesh size was 1cm. The larger hoop (turtle net; Memphis Net and Twine; [www.memphisnet.net](http://www.memphisnet.net)) consisted of three 88-cm diameter metal rings and one 31-cm diameter stretchable funnel. Overall trap length was 245 cm, and square mesh size was 2.5 cm.

The collapsible box traps and sea bass traps were purchased from Memphis Net and Twine ([www.memphisnet.net](http://www.memphisnet.net)). 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 was 2.5cm. Small box traps were 59 cm x 43 cm x 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 x 60 cm x 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 x 64 cm x 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.

All traps were baited with sardines and/or fresh fish. Traps were checked at least once every 24 hrs, 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. Aquatic habitats at Gus Engeling WMA varied in their extent based on seasonal and annual rainfall. The type and number of traps set was dictated by the amount of water available, depth of available water, and number of nets available at that time.

All turtles captured were identified to species and number of individuals recorded. Each turtle was given an individual mark, either by notching or drilling marginal scutes, and/or the implementation of a PIT tag (Biomark, 12.5 mm; [www.biomark.com](http://www.biomark.com)). For snapping turtles a hole was drilled in a marginal scute to denote a previous capture and a PIT tag was injected along the thigh of the left rear leg. A PIT tag was injected along the thigh of the left rear leg of softshell turtles. All Emydids and Kinosternids were given unique marks by notching marginal scutes with a Dremel tool ([www.dremel.com](http://www.dremel.com)). All turtles were sexed, and basic morphometric measurements, such as mass and mid-line carapace length (MCL) were recorded. The presence of damage resulting from human related activities (vehicle collisions, shooting) and/or attempted predation (teeth marks and shell and limb damage) was recorded.

I used  $X^2$  tests to determine if adult sex ratios differed from 1:1, and used t-tests to compare sizes between sexes.

*Community analysis.*— To measure the relative amount of habitat overlap between species at Gus Engeling WMA, I 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 species A and species K and S is the number of species. Niche overlap was calculated using EcoSim (Gotelli and Entsminger, 2001). Habitat type was characterized 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 canopy, heavily vegetated water bodies associated with smaller feeder creeks, springs and bogs); Pond (small manmade water bodies and borrow pits  $\leq 100\text{m}$  diameter); or Lakes (larger, several ha manmade water bodies).

To address important biotic and abiotic factors driving community composition of aquatic turtles at each trap set, I measured a suite of five structural variables: canopy cover, depth, flow, basking availability, and emergent vegetation. Canopy cover was recorded at the trap using a concave forestry densitometer (Lemmon, 1957). Depth was recorded at the opening of the trap gear. Flow was also recorded at the opening of the trap gear using a handheld flow meter averaging current speed at 5 points within the water column. Basking site availability was recorded as the percentage of exposed

surface (bank, emergent woody debris) present within a 25-m diameter area surrounding the trap. Emergent vegetation was recorded as the percentage of aquatic vegetation present within a 25-m diameter area surrounding each trap.

I 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 I measured, I 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).

I then used canonical correspondence analysis (CCA), a direct gradient analysis (Palmer, 1993; ter Braak and Verdonschot, 1995), to fit 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 as the independent variables (Palmer, 1993). Canonical correspondence analysis allows one to examine the effect of environmental variables on patterning communities. However, results from 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).

Both CA and CCA were performed using CANOCO version 4.5 (ter Braak, 1987) with default settings. Bi-plot scaling emphasized inter-species distances. Monte-Carlo permutation tests were run to identify which of the measured variables were the most important in determining the ordination.

*Comparison between sites.*—To investigate variation in species composition between the two WMA's, I compared species richness, similarity of the turtle community, and niche overlap among turtle species between Gus Engeling and Keechi Creek WMA's. Species richness was defined as total number of species captured at each site. Keechi Creek was only sampled on 4 occasions in June and July of 2009. As there waeres unequal sampling efforts between sites, I calculated richness, similarity, and niche overlap three different ways. I calculated all three parameters for Gus Engeling for all sampling periods (2006-2009), and June and July 2009 only. Calculations were also made after stratifying sampling effort at Gus Engeling by net type and number surrounding sampling dates at Keechi Creek.

I calculated a measure of similarity between sites using Sorenson's Qualitative Index:  $C_s = 2j/(a+b)$  where  $j$  = the number of species common to both sites,  $a$  = the number of species in site A, and  $b$  = the number of species in site B (Magurran, 2004). As a second measure focusing on species abundances, I also calculated Sorenson's Quantitative Index:  $C_N = 2j_N/(a_N + b_N)$  where  $a_N$  = the number of individuals in site A,  $b_N$  = the number of individuals in site B, and  $j_N$  = the sum of the lower of the two abundances of species which occur in the two sites (Magurran, 2004). Because Keechi Creek WMA was only sampled in June-July 2009, the quantitative measure was

calculated using only individual abundances collected during the same time period at Gus Engeling WMA. I used Pianka's Index of Niche Overlap to measure the relative amount of habitat overlap between species between WMAs. Niche overlap was calculated using both the entire turtle species assemblages from both WMAs, and also a dataset containing only the species shared with both WMAs. t-tests were used to compare body sizes (carapace length) of species shared between WMAs. I set  $\alpha = 0.05$  for all comparisons.

## Results

I sampled Gus Engeling WMA between mid-April and August 1 during 2006-2009 for 1,239 net nights (Table 3.1). Of 651 total captures, there were 527 individuals of 8 species of turtles (Table 3.2). Catch per unit effort at GEWMA was 0.60 turtles/net night for 2006-2009. Not all species were represented equally, and not all individuals were captured in nets. Some individuals were captured crossing roads or nesting (17 captures); these were excluded from analyses based on trap-nights as the sample unit. Although I observed river cooters 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 only included when comparing similarity indices between sites.

Sliders had 1:1 male: female sex ratio (1.00:1.02 M:F,  $n=348$ ,  $X^2_1 = 0.05$ ,  $P = 0.80$ ; Table 3.3). Sliders also exhibited significant sexual size dimorphism, with females larger than males ( $t_{403} = -10.17$ ,  $P \leq 0.001$ ; Table 3.3). Common musk turtles had a



Table 3.1: Total number of trap nights x trap type x macrohabitat at Gus Engeling Wildlife Management Area, Anderson County, TX (2006-2009) and Keechi Creek Wildlife Management Area, Leon County, TX (2009).

Trap Type	Habitat Type				
	Creek	Backwater	Marsh	Pond	Lake
GEWMA					
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
KCWMA					
Large Fyke	0	4	-	-	-
Small Fyke	1	3	-	-	-
Mini-hoop	0	0	-	-	-
Large Hoop	20	13	-	-	-
Large Box	6	15	-	-	-
Small Box	4	12	-	-	-
Dome	0	0	-	-	-

Table 3.2: Catch per unit effort by habitat type at Gus Engeling and Keechi Creek Wildlife Management Areas, Anderson and Leon counties, Texas, 2006-2009.

Species	Total Captures	Creek	Backwater	Marsh	Pond	Lake
GEWMA						
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
KCWMA						
Common Snapping Turtle	4	0	0.09	-	-	-
Alligator Snapping Turtle	3	0.03	0.04	-	-	-
Razorback Musk Turtle	4	0.06	0.04	-	-	-
Spiny Softshell	6	0.10	0.06	-	-	-
Slider	83	0.26	1.59	-	-	-

female-biased sex ratio, (1:2.66 M:F,  $n = 22$ ,  $X^2_I = 4.54$ ,  $P \leq 0.001$ ; Table 3.3). Mean MCL for male razorback musk turtles was 123.5 cm and was significantly larger ( $t_{44} = 3.97$ ,  $P \leq 0.001$ ) than the 106.0 cm mean MCL of females (Table 3.3). Mean MCL for female common musk turtles was 76.4 cm and was significantly larger ( $t_{23} = -3.56$ ,  $P \leq 0.001$ ) than the 56.4 mean MCL of males (Table 3.3). There were not enough data to calculate sex ratio or size dimorphism for spiny softshells and alligator snapping turtles (Table 3.3).

Table 3.3: Number of turtle captures for each species, by sex, and mid-line carapace lengths (MCL) at Gus Engeling Wildlife Management Area, Leon County, Texas, 2006-2009.

Species	Juvenile			Male			Female		
	n	Mean MCL	range	n	Mean MCL	range	n	Mean MCL	range
Common Snapping Turtle				14	260.8	144.9-319.0	11	243.3	185.6-288.0
Alligator Snapping Turtle	12	206.7	44.1-287.0				1	319	
Eastern Mud Turtle	1	40		13	84.7	70.6-94.5	8	88.1	68.9-104.6
Razorback Musk Turtle	5	46.5	31.1-58.9	18	123.5	86.0-139.9	28	106.0	81.3-136.8
Common Musk Turtle	1	33.0		6	56.4	42.4-66.4	19	73.4	50.7-88.7
Spiny Softshell Turtle	1	60.9					10	351.4	264.7-476.0
River Cooter	1	132.8		1	242.4		3	273.1	261.2-282.2
Slider	59	74.7	34.4-128.4	162	165.6	99.4-246.8	166	202.1	104.3-266.4

*Community analysis.*—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 (Figure 3.2). Eastern mud turtles had higher scores on the second axis, and alligator snapping turtles higher scores on the first axis (Fig.3.2).

Inclusion of environmental gradients within a CCA resulted in a strong gradient influenced by flow, depth, and basking structure, and a secondary gradient influenced mostly by vegetation and canopy cover (Fig. 3.3). The percent 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 greater 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 shallower water and high percentages of emergent vegetation. Razorback musk turtles, alligator snapping turtles, and spiny softshell turtles occupied sites with increasing flow. Locations of species scores represented a transition of species among lentic and lotic habitats, with more emergent vegetation and decreasing depth separating lentic habitats and the species associated with lentic habitat (Fig. 3.3). Although vegetative/flow gradients are apparent (Fig. 3.3), Monte Carlo permutation tests revealed that depth and presence of basking structure were the variables most strongly associated with species distributions.

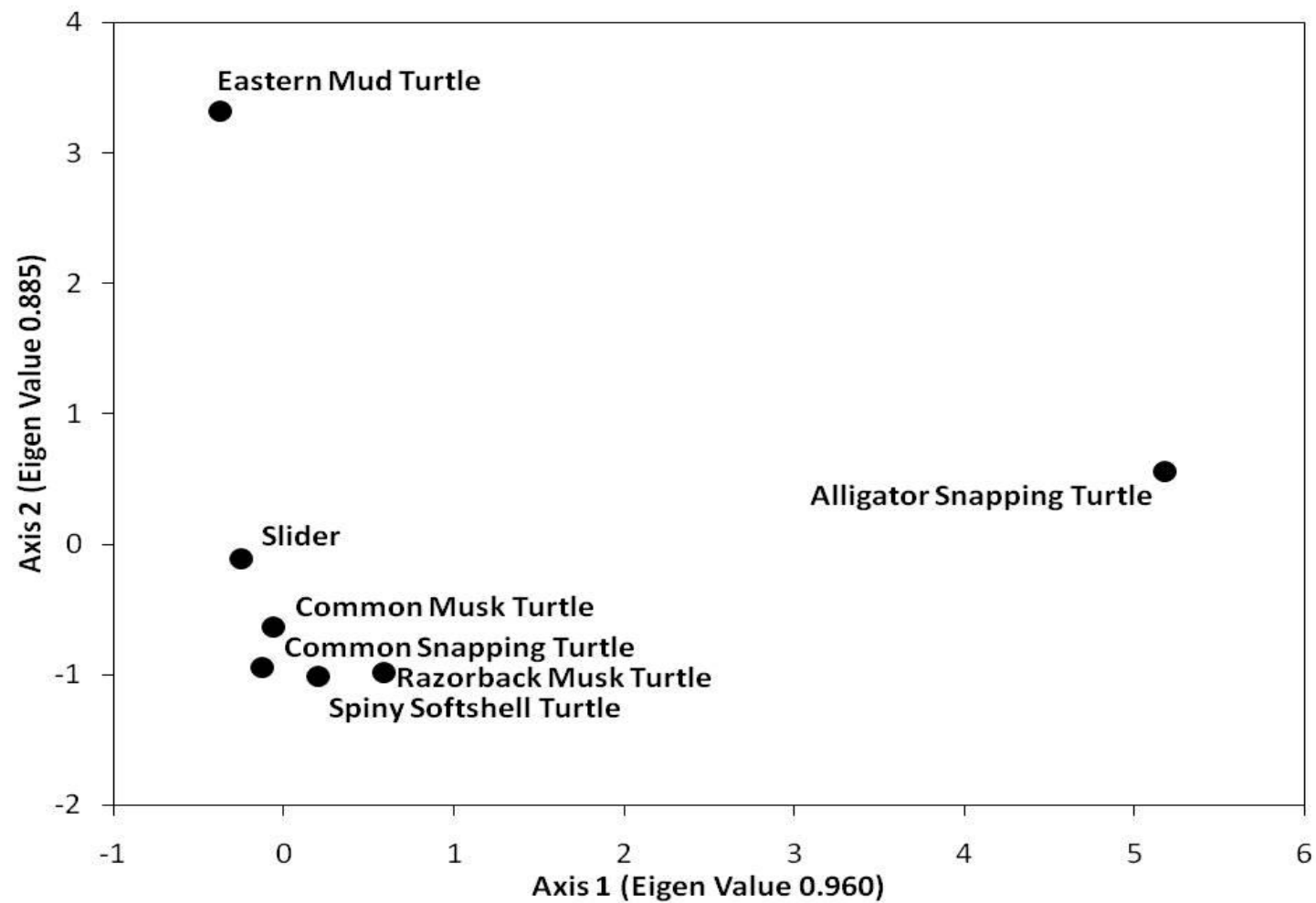


Figure 3.2. Distribution of species scores based on the first and second axes from Correspondence Analysis for aquatic turtles at Gus Engeling WMA. Total inertia for all axes is 4.98.

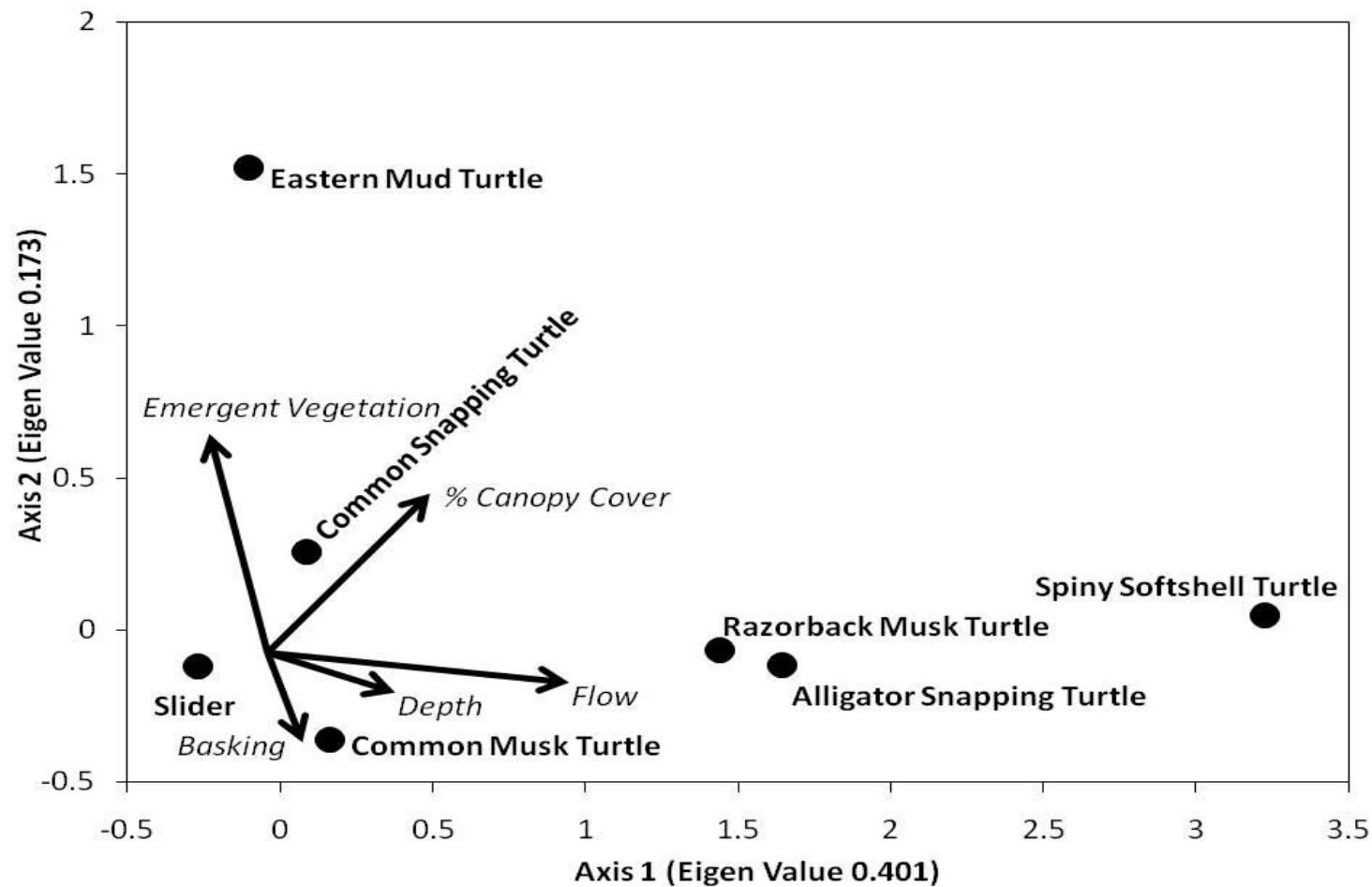


Figure 3.3. Ordination of aquatic turtle species from Gus Engeling WMA based on Canonical correspondence analysis using species abundance and environmental variables (only the first two gradients are shown). Contributions of environmental variables to each gradient are represented by vectors. Total inertia for all axes is 4.983.

Niche overlap ranges from 0.0 to 1.0, with higher values reflecting increasing overlap of resources. Overlap of resource use was high between alligator snapping turtles, spiny softshell turtles, and razorback musk turtles (Table 3.4), species associated with higher flow in Fig. 3.3. A similar degree of overlap was also seen between sliders and common snapping turtles (Table 3.4). Common musk turtles had moderate to high overlap with all species, while eastern mud turtles had low overlap with all species (Table 3.4). 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 (Table 3.4). The two species of chelydrids, common snapping turtles and alligator snapping turtles, had a moderate degree of overlap in habitat use (Table 3.4).

*Comparison between sites.*—Keechi Creek WMA was sampled in June and July of 2009 for 78 net nights (12 small box, 16 large box, 24 large hoops, 3 small fyke, 2 large fyke nets) (Table 3.1) resulting in 110 captures of 94 individuals of 5 species of turtles (Table 3.2). Catch per unit effort at Keechi Creek WMA in 2009 was 1.41 turtles/net night. At Gus Engeling WMA during the same general time period, seventy-eight net nights, stratified by net type, captured 20 individuals of 3 species of turtles [common snapping turtle (n=2), common musk turtle (n=3), and slider (n=15)], with a catch per unit effort of 0.25 turtles/net night. Total catch per unit effort at Gus Engeling WMA for the entire 2009 season was 0.23 turtles/net night. Because of low capture rates

Table 3.4: Habitat niche overlap (Pianka, 1973) amongst turtle species at Gus Engeling Wildlife Management Area, Anderson County, Texas, 2006-2009.

	Spiny Softshell turtle	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



Table 3.5: Comparison of mean mid-line carapace lengths (mm) ( $\pm 1$  standard error) between Gus Engeling Wildlife Management Area and Keechi Creek Wildlife Management Area, Anderson and Leon counties, Texas, 2006-2009.

Species	GEWMA			KCWMA			<i>t</i>	<i>P</i>
	n	MCL	SE	n	MCL	SE		
Spiny Softshell Turtle	10	351.4	55.9	8	394.3	62.6	1.532	0.072
Common Snapping Turtle	25	253.2	15.9	5	279.9	37.2	1.340	0.095
Alligator Snapping Turtle	13	227.9	53.4	3	239.3	55.5	0.332	0.372
Razorback Musk Turtle	46	112.9	16.7	4	113.8	20.5	0.109	0.456
Male Sliders	215	165.7	32.1	56	178.4	24.8	3.193	0.001
Female Sliders	215	202.1	41.5	19	213.3	27.22	1.627	0.057

at Gus Engeling WMA, I used all 2009 captures (216 specimens, 8 species) for comparisons of species assemblages between sites.

Sliders were the only species recaptured with enough frequency at both sites to compare recapture rates. Recapture rates at Gus Engeling WMA were 30% (38% M: 23% F) and 24% Keechi Creek WMA (26% M: 19% F).

Mid-line carapace lengths for male and female sliders were significantly larger at Keechi Creek WMA than at Gus Engeling WMA (Table 3.5). Spiny softshell turtles and common snapping turtles were larger, although not significantly so, at Keechi Creek WMA than at Gus Engeling WMA (Table 3.5). There were no differences in size in alligator snapping turtles, or razorback musk turtles between the two WMA's (Table 3.5).

Keechi Creek WMA had lower habitat heterogeneity, with only two major habitat types present (Creek and Backwater) compared to five for Gus Engeling WMA. All species captured at Keechi Creek WMA were also captured at Gus Engeling WMA. River Cooters, common musk turtles, and eastern mud turtles were captured at Gus

Engeling WMA, but not Keechi Creek WMA. The Sorenson qualitative index, based on presence/absence of species was 0.625, showing moderate similarity in species composition between WMAs. Using species abundances, Sorenson's quantitative index based on abundances was much higher (0.959).

The two WMAs had similar turtle species composition, but species richness was greater at Gus Engeling. Habitat niche overlap was higher among turtles at Keechi Creek WMA (0.869) than those at Gus Engeling WMA (0.590). The niche overlap value just for those species that were captured at both sites was 0.651.

Signs of attempted predation were higher at Gus Engeling WMA than Keechi Creek WMA. At Gus Engeling WMA, teeth marks from predators (conical punctures, usually found on both the carapace and plastron) were observed on 25% of the sliders, 40% of river cooters, 27% of eastern mud turtles, 11% of common musk turtles, and 4% of razorback musk turtles. An additional 7 sliders at Gus Engeling WMA were missing limbs. Only 7% of sliders at Keechi Creek WMA exhibited teeth marks. One common snapping turtle at Keechi Creek WMA had a large triangular piece of carapace missing. This notch matched injuries inflicted upon common snapping turtles by alligator snapping turtles in Kansas (Shipman *et al.*, 1994). Human related injuries were low. One slider at Gus Engeling WMA had a bullet wound, while another showed shell damage that may have resulted from being run over by a vehicle.

## Discussion

My 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* sp.), were not captured during my 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 Gus Engeling WMA, I was 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.

Adult sex ratios for sliders at both sites were male biased, which is generally the rule for most well studied slider populations (Ernst and Lovich, 2009). Gibbons (1990) listed several environmental and physiological factors that could drive sex ratios in sliders, but warned that sampling bias may also affect reported sex ratios. This may be partially the case here, given that male sliders had higher recapture rates than females.

Mahmoud (1969) reported female-biased sex ratios for razorback musk turtles in Oklahoma, and the species is sexually dimorphic, with males being the larger sex (Tinkle, 1958; Iverson, 2002), which mirrored results from my survey at Gus Engeling WMA. Female common musk turtles tend to be larger, which was true at Gus Engeling WMA, although sex ratios vary greatly from population to population (Ernst and Lovich, 2009). Secondary sex characteristics in male common musk turtles occurred at carapace lengths that were nearly 1 cm smaller than values previously reported in the literature

(Risley, 1933; Tinkle, 1961; Mitchell, 1988). The cause of the smaller size at maturity at Gus Engeling WMA is unknown, but is ripe for further study considering the complexity of an environment that includes two other sympatric species of Kinosternid and American alligators.

Captures of alligator snapping turtles were low at both sites and were represented by small individuals. Only one individual at each site was large enough to be considered sexually mature, although one hatchling (44.1 mm MCL) was captured at Gus Engeling WMA in April 2009. The stretch of Catfish Creek that flows through GEWMA is fairly shallow, which may preclude the occurrence of larger individuals (Sloan and Taylor, 1987; Riedle *et al.*, 2006; Shipman and Riedle, 2008). Larger individuals have been captured on the site, and an unpublished survey conducted in the late 1990's captured two larger individuals (392 and 403 mm MCL) at Gus Engeling WMA and eight individuals between 304 and 582 mm MCL at Keechi Creek WMA (Lee Fitzgerald, Texas A&M University Pers. Comm). There is some evidence that Catfish Creek has become shallower over time due to siltation (D. Synatzske, TPWD, Pers. Comm.). Deeper habitats were present at Keechi Creek WMA, and based on bite marks on one individual of common snapping turtle, larger individuals of alligator snapping turtles may be present there. Of particular note is the capture of an alligator snapping turtle in an upland lake at Gus Engeling WMA. The lake drains into Catfish Creek suggesting a short upstream movement followed by an overland crossing of ~20 m, or a release by humans.

Alligator snapping turtles have experienced intensive harvest and subsequent declines throughout their range (Pritchard, 1989). The presence of only young turtles may also be a symptom of current or past perturbations of harvest. Size disparities have been observed between harvested and unharvested populations in Arkansas (Trauth *et al.*, 1998), Georgia (Jensen and Birkhead, 2003), Missouri (Shipman and Riedle, 2008), and Oklahoma (Riedle *et al.*, 2005).

Correspondence Analysis resulted in a clustering of several species at Gus Engeling WMA. Although each of these species has specific habitat requirements, they overlap in their use of available habitats at Gus Engeling WMA (Table 3.4). The exception was the eastern mud turtle that was largely restricted to shallow, heavily vegetated habitats, a pattern reported in other studies (Buhlmann and Gibbons, 2001). Ordination of the alligator snapping turtle along environmental gradients was intriguing. Although this species shared habitat with several species, they were segregated from other species along Axis 1 (Fig. 3.2). Alligator snapping turtles consume a wide variety of prey, including other species of turtles (Pritchard, 1989; Ernst and Lovich, 2009) and agnostic/predatory behavior towards large individuals of common snapping turtles has been reported (Shipman *et al.*, 1994). Because individual nets were considered a “site” within my analyses, the presence of a large predatory turtle within a net (or site) could have excluded other turtles (Cagle and Chaney, 1950) thus biasing CA results with respect to this predator.

Canonical correspondence analysis results largely match what is known about the natural history of turtle species at these sites. Sliders are considered ecological

generalists and are typically captured in diverse aquatic habitats (Ernst and Lovich, 2009). Within my ordination analyses, sliders were positioned fairly close to the intersection of both axes (Fig. 3.3), 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 typically associated with sites characterized by 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 Gus Engeling WMA, allowing for a comparison of habitat use when in sympatry. In Oklahoma, razorback musk turtles and common musk turtles are frequently found together, but are rarely found with eastern mud turtles. Razorback and common musk turtles prefer flowing water, whereas eastern mud turtles prefer vegetated, lentic bodies of water (Mahmoud, 1969). Even though all three occurred within a small area in this study, they revealed similar patterns of habitat segregation with eastern mud turtles being found in heavily vegetated marshes, whereas the two *Sternotherus* species were associated with greater depth and flow. Eastern mud turtles are physiologically adapted to the ephemeral nature of their habitat, because they can estivate during prolonged dry periods (Ernst and Lovich, 2009). Razorback and common musk turtles prefer deeper, more permanent aquatic habitats; these turtles exhibit high rates of evaporative water loss that restricts terrestrial activity and ability to estivate (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 revealed some segregation in habitat use. 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 bodies of water (Ewert *et al.*, 2006). Both species are large predators/scavengers; therefore, competition for food resources and predation upon one another may be driving the spatial distribution of both species 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).

The two WMAs had similar turtle community composition, but use of available habitat appeared to differ in many cases. The relatively low species richness in these two WMAs appears to be related to absence of certain types of habitats, primarily open canopy, heavily vegetated marshes, and possibly competition. At Gus Engeling WMA both river cooters and eastern mud turtles were predominantly captured or observed in those habitats. The absence of common musk turtles at Keechi Creek WMA is notable, because suitable habitat was present. One hypothesis is that common musk turtles are competitively excluded by razorback musk turtles.

Differences in capture rates and body size between Gus Engeling WMA and Keechi Creek WMA also might reflect differences in natural and anthropomorphic

perturbations. Introduced predators such as feral hogs (Fordham *et al.*, 2006; Doupe *et al.*, 2009) and fire ants (*Solenopsis invicta*; Moulis, 1997; Allen *et al.*, 2001; Buhlmann and Coffman, 2001) are known to have significant impacts on turtle nests and adults in terrestrial refugia. Raccoons are a well known predator of turtles (Ernst and Lovich, 2009) and high population densities of raccoons are known to significantly skew turtle populations to primarily older age classes with low to no recruitment (Browne and Hecnar, 2007).

Gus Engeling WMA had additional impacts that are not present at Keechi Creek WMA. These include predation pressure by alligators and human impacts, such as higher road density and fishing with set lines (limb lines, trot lines). Road mortality can have a large impact on population structure and persistence of turtle populations, and female turtles are most frequently hit during movements for nesting (Gibbs and Steen, 2005). Based on my four years of sampling at Gus Engeling WMA, incidence of road mortality was very low, but it should be considered given that several female sliders were captured while nesting along roadways. Of greater concern is the high density of set lines for fishing, most of which appeared to be untended. Set lines are effective gear for catching turtles (Lagler, 1943; Moll and Moll, 2004) and can negatively impact aquatic turtle populations (Smith, 1979; Shipman and Riedle, 2008).

Alligators exhibit complex relationships with turtles, and these include positive interactions through habitat and reproductive facilitation (Dietz and Jackson, 1979; Bondavalli and Ulanowicz, 1999) and negative interactions in the form of competition and predation (Gibbons and Lovich, 1990; Bondavalli and Ulanowicz, 1999). American



alligators can have a significant impact on body size distributions and population densities of aquatic turtles (Gibbons and Lovich, 1990; Bondavalli and Ulanowicz, 1999; Aresco and Gunzburger, 2007). Turtles at Gus Engeling WMA had a higher proportion of injuries related to attempted predation by American Alligators and other predators.

Chesson (2000) suggested that local-scale processes influence assemblage structures because different species have fitness advantages affected by abiotic environment and densities of conspecifics that in turn influences regional species assemblages (Michalet *et al.*, 2002; Urban *et al.*, 2008). Turtle communities at Gus Engeling and Keechi Creek WMAs were similar, but there were considerable differences in patterns of abundances and habitat use. These differences may be related to habitat heterogeneity, long-term changes in local habitat, and natural and anthropogenic perturbations. Increasing the scale of sampling to include additional sites within the Middle Trinity River Basin would better elucidate the role of these factors in determining turtle community structure.

# CHAPTER IV

## TRAPPING EFFICIENCY FOR AQUATIC TURTLES IN EAST TEXAS

### Introduction

Species inventories and acquisition of voucher specimens are important when making comparisons of distribution and abundance over a temporal scale (Heyer *et al.*, 1994). Thus, baseline inventories are a routine part of any environmental assessment (Gibbons *et al.*, 2000). Within the Chelonia, baseline information on the biology of many species is lacking (Lindeman, 2008). Naturally, the success of baseline inventories is dependent on the application of appropriate field sampling techniques. As such, periodic evaluation of the efficacy of sampling techniques merits attention by researchers. Understanding of the contribution of complementary methods to sampling biodiversity is also important because multiple sampling methods are often needed in order to adequately sample diverse communities. For example, in a comparison of seven sampling methods for amphibians, Gunzburger (2007) found that detection probability varied across a range of techniques depending on species and life stages. Greatest species richness was documented through use of frogloggers, while active sampling (dipnets, box traps) provided a more accurate count of individuals.

Early collecting methods for aquatic turtles included antiquated (or just improper) techniques such as shooting, as well as more time-honored methods of using modified hoop nets and fyke nets (Ruthven, 1912; Lagler, 1943). Each method used for

sampling may show biases in captures among species (Cagle and Chaney, 1950; Vogt, 1980), age classes, and sexes (Ream and Ream, 1966; Koper and Brooks, 1998; Smith and Iverson, 2002), thus a combination of techniques may be needed when sampling diverse species assemblages.

Cagle and Chaney (1950) described species specific variation in capture efficacy during their work on Louisiana turtle communities. They noted that larger turtles, such as snapping turtles (*Chelydra* and *Macrochelys*), may preclude other turtles from entering the trap. They also noted that river cooters (*Pseudemys concinna*) were only captured by hand, while false map turtles (*Graptemys pseudogeographica*) were only captured in traps. Sterrett *et al.* (2010) compared effectiveness of active sampling (snorkeling) versus passive sampling (baited hoop traps) among several turtle species in a clear water Georgia stream. They found differences in capture probabilities between methods as Barbour's map turtles (*Graptemys barbouri*) were captured 90% of the time by snorkeling, while pond sliders (*Trachemys scripta*) were captured 88% of the time in baited hoop nets.

Previous research documented variation in capture rates among sites as well as among species. Ream and Ream (1966) noted that painted turtles (*Chrysemys picta*) in Wisconsin had female biased capture rates using basking traps, male biased captured rates using baited hoop nets, and equal sex ratios when captured by hand or dip net. However Vogt (1980) reported equal sex ratios utilizing fyke nets in Wisconsin. Female biased captured rates of painted turtles, regardless of technique, were recorded by Koper and Brooks (1998) in Ontario, Canada.

Not all land managers/researchers can afford a wide range of sampling gear, as trap types for aquatic turtles vary widely in cost (\$30-1000), which would impose limitations on the number of techniques they could deploy (Plummer 1979; Sterrett *et al.*, 2010). Evaluation of sampling methods should include the effectiveness in terms of number of species and individuals collected in relation to associated labor and cost (Corn *et al.*, 2000).

I sampled two sites in eastern Texas as part of a community ecology study focused on aquatic turtles between 2006-09 with the support of the Texas Parks and Wildlife Department. Results from this research support the need to better understand and conserve biodiversity on lands managed by the agency. In response to assisting them with future monitoring efforts, I reviewed my trapping results after the fact to compare capture efficacy, effort, and detection probability for each trap type and similarity of captures between trap types. Considering that area managers at this site would most likely have limited funds for future monitoring, I wanted to determine which trap type or combination of trap types would provide adequate capture rates for sampling the entire assemblage of aquatic turtles at this site.

### Study Area

The Trinity River originates north of the Dallas/Fort Worth metroplex in northeastern Texas, and flows 1150 km southward to empty into Galveston Bay on the Gulf Coast. The Trinity River Basin lies solely within Texas encompassing 46,540 km<sup>2</sup> and roughly one-third of the state's population (Huser, 2000). Annual rainfall is

approximately 100 cm/yr (Johnson, 1931), and the drainage experiences frequent flooding, particularly within its upper reaches (Huser, 2000). Because there are major urban centers in the Middle Trinity River Basin, the stretch of river between Dallas/Fort Worth and Houston is considered an area of concern by the Texas Parks and Wildlife Department (Bill Adams, Texas Parks and Wildlife Department pers. com.). The Middle Trinity River Basin encompasses the Texas Natural Regions of the East Texas Plains and the Prairies Province, and the bisection of moderately humid grasslands and humid cross-timbers habitats by the Trinity River results in high species richness of both flora and fauna (Johnson, 1931).

My primary study area was located in Anderson County, Texas, on the Texas Parks and Wildlife Department managed Gus Engeling Wildlife Management Area (WMA) (Fig. 3.1 previous chapter). Gus Engeling WMA is a 4,434-ha property encompassing a large portion of the Catfish Creek ecosystem. Catfish Creek is a tributary in the Middle Trinity River Basin, encompassing 730 ha and 32 km of Anderson and Henderson counties and considered a Natural National Landmark (Telfair, 1988). Twenty-four small creeks feed Catfish Creek, most of which are spring fed. Habitats associated with the Catfish Creek Ecosystem include by post-oak savanna, bottomland hardwoods, marshes, swamps, bogs, and springs. Aquatic habitat at Gus Engeling WMA is represented by Catfish Creek and its tributaries, adjacent scours and backwater habitat, open canopy marshes, several small ponds and larger lakes. Aquatic habitat is augmented by a series of levees and flood-control gates, built in cooperation with Ducks Unlimited, to provide wetlands for waterfowl. In addition, there are several

ponds or “borrow” pits associated with the levees (Eric Wolverton, Texas Parks and Wildlife Department pers.com.).

My second site was the TPWD managed Keechi Creek WMA in northeastern Leon County, Texas. Keechi Creek WMA, a small 607 ha management area, also lies within the Middle Trinity River Basin and was acquired by TPWD in 1986 (Fig. 3.1). Aquatic habitats at Keechi Creek WMA are much less complex, consisting of Keechi and Buffalo creeks, and a large oxbow lake associated with Keechi Creek. The oxbow lake is intermittently connected to both creeks (Gelwick *et al.*, 2001). Terrestrial habitat is predominately bottomland hardwoods. Hardwoods in this region are typified by green ash (*Fraxinus pennsylvanica*), boxelder (*Acer negundo*), bur oak (*Quercus macrocarpa*), Shumard oak (*Q. shumardii*), overcup oak (*Q. lyrata*), water oak (*Q. nigra*), willow oak, (*Q. phellos*) and post oak (*Q. stellata*); (Ryberg *et al.* 2004).

## Methods

I sampled aquatic habitats at Gus Engeling WMA between late May and late July, 2006-2008, and between April and late July 2009. I divided trap types into deep water and shallow water trap gear. Deep water gear consisted of two sizes of fyke nets, and large diameter hoop nets. Shallow water gear consisted of mini catfish hoop nets, two sizes of square collapsible fish traps and one size of sea/bass/dome traps.

The large fyke net (Christensen Nets, Everson, WA, USA; [www.christensennetworks.com](http://www.christensennetworks.com)) was 4.5 m in length (front frame to cod end) with a single 14.5 m x 88 cm lead. The two anterior rectangular frames were 120 cm x 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, WA, USA; [www.christensennetworks.com](http://www.christensennetworks.com)) was 3.3 m in length from the front frame to cod end, and had a single 7.4 m x 67 cm lead. The two rectangular front frames were 95 cm x 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. Square mesh size was 1cm. The larger hoop (turtle net; Memphis Net and Twine, Memphis, TN, USA; [www.memphisnet.net](http://www.memphisnet.net)) consisted of three 88-cm diameter metal rings and one 31-cm diameter stretchable funnel. Overall trap length was 245 cm, and square mesh size was 2.5 cm.

The collapsible box traps and sea bass traps were purchased from Memphis Net and Twine (Memphis Net and Twine, Memphis, TN, USA; [www.memphisnet.net](http://www.memphisnet.net)). 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 was 2.5cm. Small box traps were 59 cm x 43 cm x 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 x 60 cm x 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 x 64 cm x 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.

All traps were baited with sardines and/or fresh fish. Traps were checked at least once every 24 hrs. Sampling gear was set so that some portion was exposed above the water surface, providing air space for turtles and other air breathing organisms.

Aquatic habitats at Gus Engeling WMA were highly variable in size, based on seasonal and annual rainfall. The type and number of traps set was dictated by the amount of water available, depth of available water, and number of nets available at that time. I measured depth at the opening of each trap. To relate habitat characteristics and depth to the trap type used I first classified five types of habitat at Gus Engeling WMA: Creek (flowing waters associated with Catfish Creek and its tributaries); Backwater (scours and flooded timber associated with the Catfish Creek floodplain); Marsh (shallow, open 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 and consisting of more open water than marshes); or Lakes (larger, several ha manmade water bodies).

Since trapability of individual species may vary by trap type, I used program PRESENCE (Hines, 2006) to calculate detection probabilities for each trap type. As a large number of observations are required to obtain reliable detection probabilities, individual turtle species were grouped by family (emydids, kinosternids, and chelydirids). The family Trionychidae was excluded because of very low capture rates. Not all trap types were used frequently throughout the project, so I only calculated detection probabilities for three trap types: large hoop nets, large box traps, and fyke nets (both large and small fyke nets combined). I also calculated catch/per unit effort x



species x habitat x trap type. A unit of effort was defined as a net night, or one net set over one night.

To compare species richness between trap types I used Jaccard's measure of similarity:  $CJ = j / (a + b - J)$  where  $j$  = the number of species common to both net types,  $a$  = the number of species in net type A, and  $b$  = the number of species in net type B (Magurran, 2004). Then I constructed species accumulation curves to look at the rate at which new species were captured using each trap type. I constructed randomized species accumulation curves and 95% confidence intervals using program EstimateS (Colwell, 2013). Program EstimateS assess species richness through construction of rarefaction curves, which are created by resampling the pool of  $N$  samples multiple times and plotting the average number of species found in each sample (Gotelli and Colwell, 2001; Chiarucci *et al.*, 2008). Samples were randomized 100 times for calculation of sample means and confidence intervals.

Not all traps were available for use in the same numbers, primarily due to cost, and this study was not originally set-up to compare capture techniques, but rather attempt to thoroughly sample an aquatic turtle community. So the number of samples for each trap type was unequal. Program EstimateS extrapolates rarefaction curves past your reference samples allowing one to compare unequal sample sets (Longino and Colwell, 2011; Colwell *et al.*, 2012). I extrapolated curves for all trap types out to 500 net nights.

I also determined sex ratio by trap type for each species to determine if there might be a sex bias for each trapping technique. To look for any observed capture bias

by body size by trap type I utilized pond sliders, our most frequently captured species, to compare body size by trap type.

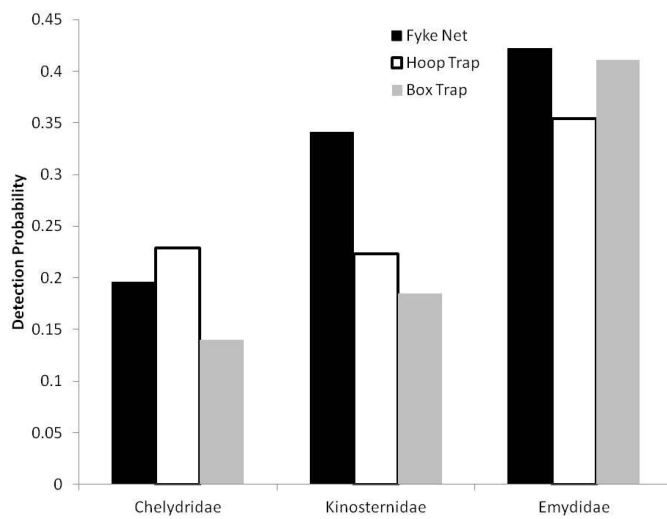
## Results

Sampling yielded 520 captures of 8 species of turtles in nets at Gus Engeling WMA (Table 4.1). Capture probabilities and detection rates varied among trap types (Table 4.1; Figure 4.1a). Emydids had the highest detection probabilities in all three net types, and fyke nets and large box traps had slightly higher detection probabilities than other trap types. Chelydrids had higher detection probabilities in large hoop nets and kinosternids had higher detectability within the fyke nets. Large fyke nets captured higher proportions of common musk turtles (*Sternotherus odoratus*). Large hoop nets captured higher proportions of spiny softshell turtles (*Apalone spinifera*), alligator snapping turtles (*Macrochelys temminckii*), and razorback musk turtles (*Sternotherus carinatus*). Large box traps captured higher proportions of common snapping turtles (*Chelydra serpentina*), eastern mud turtles (*Kinosternon subrubrum*), river cooters, and pond sliders. The two types of fyke net, large hoop traps, and large box traps were the most similar in species captured (Table 4.2). Dome and mini catfish hoop traps were also similar (Table 4.2).

Table 4.1: Catch per unit effort x trap type at Gus Engeling Wildlife Management Area, Anderson County, TX, 2006-2009. Species abbreviations: APSP, Spiny Softshell Turtle; CHSE, Common snapping Turtle; MATE, Alligator Snapping Turtle; KISU, Eastern Mud Turtle; STOD, Common Musk Turtle; STCA, Razorback Musk Turtle; PSCO, River Cooter; TRSC, Slider.

Trap Type	Net Nights	Captures	Species							
			APSP	CHSE	MATE	KISU	PSCO	STOD	STCA	TRSC
Large Fyke	82	31	0.00	0.01	0.01	0.01	0	0.13	0.03	0.25
Small Fyke	54	34	0.00	0.04	0.02	0.05	0	0.04	0.05	0.44
Mini-Hoop	58	44	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.69
Large Hoop	318	111	0.01	0.01	0.01	0.00	0.00	0.01	0.06	0.09
Large Box	547	259	<0.01	0.03	<0.01	0.03	<0.01	0.01	<0.01	0.36
Small Box	193	23	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.10
Dome	47	18	0.00	0.00	0.00	0.00	0.00	0.05	0.05	0.37
All Trap Types	1299	457	<0.01	0.01	<0.01	0.02	<0.01	0.02	0.02	0.27

**A.**



**B.**

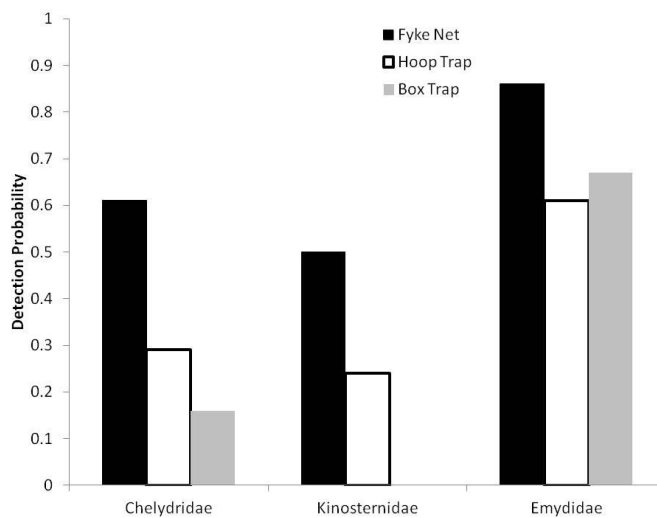


Figure 4.1. A. Detection probabilities for three families of aquatic turtles in three types of net gear at Gus Engeling WMA, Anderson County, Texas, 2006-2009. B. Detection probabilities for three families of aquatic turtles in three types of net gear at Keechi Creek WMA, Leon County, Texas.

Table 4.2: Jaccards similarity values for captures by net type at Gus Engeling Wildlife Management Area, Anderson County, Texas, 2006-2009.

Trap Type	Trap Type					
	Large Fyke	Small Fyke	Mini-Hoop	Large Hoop	Large Box	Small Box
Large Fyke						
Small Fyke	1.00					
Mini-Hoop	0.50	0.50				
Large Hoop	0.83	0.83	0.43			
Large Box	0.75	0.75	0.38	0.87		
Small Box	0.33	0.33	0.25	0.14	0.25	
Dome	0.50	0.50	1.00	0.43	0.38	0.25

The only trap type to capture all 8 species of turtles at Gus Engeling WMA were the large box traps (Table 4.3), although fyke nets and large hoop traps accumulated more species sooner (Table 4.3). Pond sliders were always the first species captured in a trap, except for the large fyke nets (Table 4.3). Fyke nets appeared to be fairly good at capturing kinosternids, although both box traps did as well.

Large box traps were the only trap type whose rarefaction curve did not reach asymptote (Fig. 4.2). Large box traps continued to add species, particularly juveniles of larger species, throughout the duration of the project (Table 4.3). Confidence intervals tend to grow dramatically around the rarefaction curves once the curve begins to extrapolate past the last reference sample (Colewell, 2013). When confidence intervals were compared to those of the other small trap types, they tend to remain narrow around small box traps, but widen considerably around the mean accumulation curve for dome traps. When comparing confidence intervals for the larger trap types, they remain large for the mini-hoop and fyke nets (Figure 4.3). Small fyke nets, mini-hoop traps and dome traps were the only trap types to reach asymptote at a greater number of species than actually captured. Results for these trap types suggests that more frequent use would result in the capture of additional species, possibly at a higher rate than other large trap types.

Table 4.3: Sequential order of species captured with number of net nights to first occurrence in parentheses by trap type at Gus Engeling Wildlife Management Area, Anderson County, TX, 2006-2009. Species abbreviations: APSP, Spiny Softshell Turtle; CHSE, Common snapping Turtle; MATE, Alligator Snapping Turtle; KISU, Eastern Mud Turtle; STOD, Common Musk Turtle; STCA, Razorback Musk Turtle; PSCO, River Cooter; TRSC, Slider.

Trap Type	Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	Species 7	Species 8
Large Fyke	KISU (2)	MATE (9)	STCA (17)	STOD (18)	TRSC (19)	CHSE (19)		
Small Fyke	TRSC (9)	CHSE (9)	KISU (10)	STCA (20)	STOD (25)	MATE (52)		
Mini-Hoop	TRSC (2)	CHSE (2)	STCA (14)					
Large Hoop	TRSC (1)	STOD (18)	STCA (24)	APSP (22)	MATE (33)	STOD (37)		
Large Box	TRSC (7)	CHSE (7)	STCA (17)	STOD (29)	PSCO (60)	KISU (103)	APSP (208)	MATE (308)
Small Box	TRSC (1)	KISU (4)						
Dome	TRSC (1)	STCA (7)	STOD (34)					

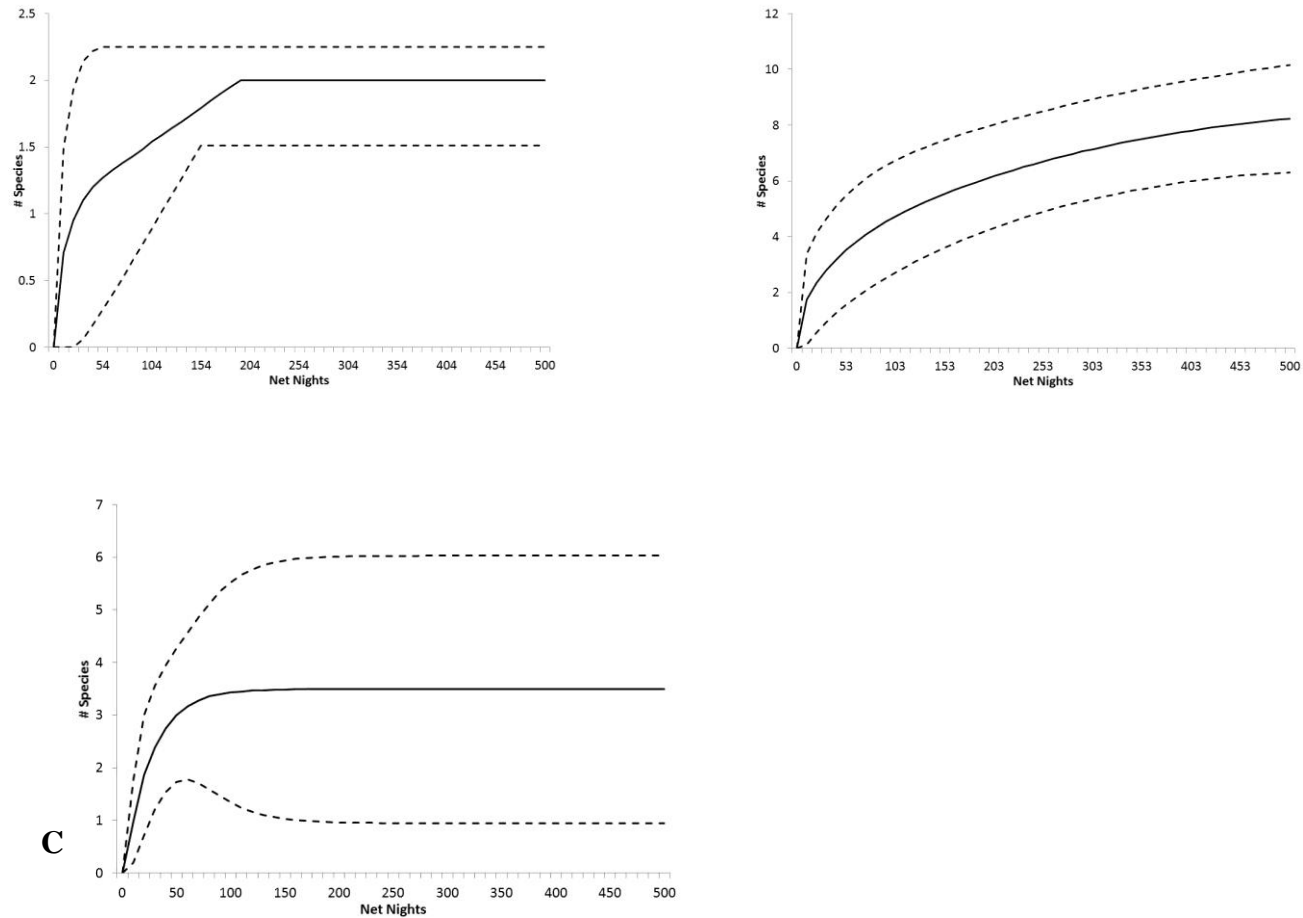


Figure 4.2. Species accumulation curves and 95% CI for (A) small box traps, (B) large box traps and (C) dome traps at Gus Engeling WMA, Anderson County, Texas 2006-2009.



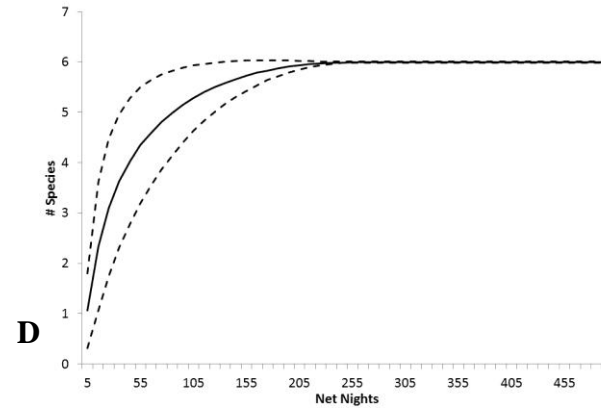
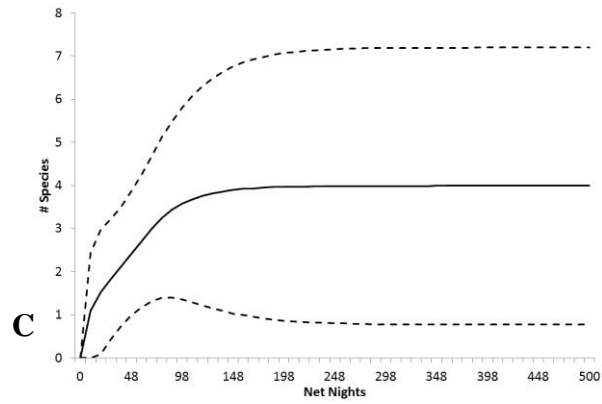
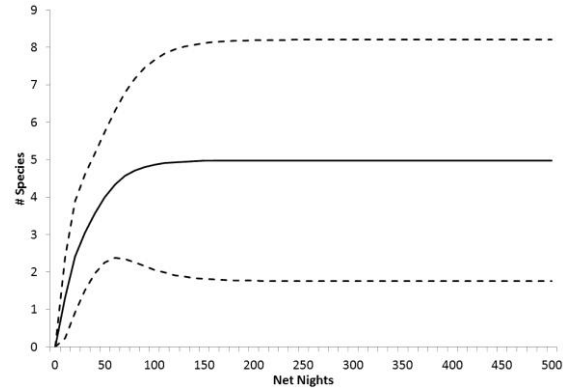
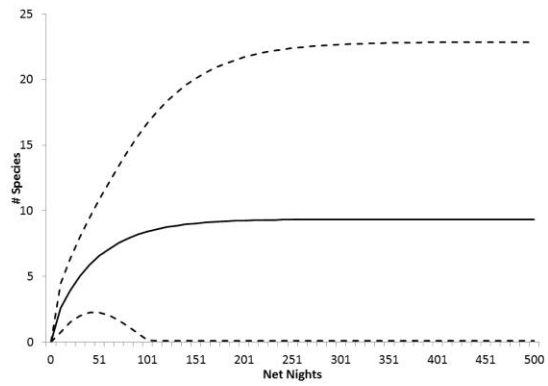


Figure 4.3. Species accumulation curves for (A) small fyke nets, (B) large fyke nets, (C) mini-hoop traps, and (D) large hoop traps at Gus Engeling WMA, Anderson County, Texas 2006-2009.

Water depth does influence where certain net types can be set, so in turn net types showed variation in capture rates in different habitats (Table 4.4). Creek habitats had deeper water ( $64.1 \pm 27.1$  cm), followed by lakes ( $49.1 \pm 44.1$  cm), ponds ( $46.7 \pm 27.4$  cm), backwater ( $36.5 \pm 26.1$ ) and marsh ( $36.2 \pm 26.4$ ) habitats. In creek habitats large fyke nets and mini-hoop traps had the highest capture rates (Table 4.4). Mini-hoop traps and large box traps had high capture rates in shallow backwater habitats, while small fyke nets and dome traps did well in more heavily vegetated marshes (Table 4.4). Both types of fyke net, large box traps and mini-hoops had high capture rates in ponds and lakes (Table 4.4).

Mean mid-line carapace lengths for pond sliders were not significantly different among different trap types at Gus Engeling WMA ( $df = 6$ ,  $F = 9.17$ ,  $P = 2.68$ ). All sizes of pond sliders were captured in all trap types, although the median size for turtles captured in small box, dome, and mini-hoop traps were slightly smaller than those captured in other traps (Fig. 4.4).

Although sampling effort was considerably less at Keechi Creek WMA, I observed differences in detectability among trap types when compared to Gus Engeling WMA. At this site, emydids had higher detection rates than other families, and detection rates for chelydrids and kinosternids were similar (Fig 4.1b). The lack of captures of kinosternids in box traps at Keechi Creek WMA may be reflective of the absence of common musk turtles and eastern mud turtles in our captures at this site (Table 4.5).

Table 4.4: Catch per unit effort x trap type x habitat at Gus Engeling Wildlife Management Area, Anderson County, Texas 2006-2009. Traps were ranked in order of highest catch per unit effort for each habitat type sampled.

Trap Type	Creek	Rank	Backwater	Rank	Marsh	Rank	Pond	Rank	Lake	Rank
Large Fyke	0.66	1	0.18	5	0.20	5	1.00	3	0.60	4
Small Fyke	0.44	3	0.18	5	0.80	2	1.37	2	1.33	2
Mini-hoop	0.54	2	0.80	1	0.00	6	1.5	1	1.57	1
Large Hoop	0.15	6	0.21	4	0.00	6	0.23	6	0.59	5
Large Box	0.23	4	0.48	2	0.27	4	0.42	5	1.25	3
Small Box	0.00	7	0.16	6	0.53	3	0.00	7	0.25	6
Dome	0.18	5	0.33	3	0.83	1	0.88	4	-	-

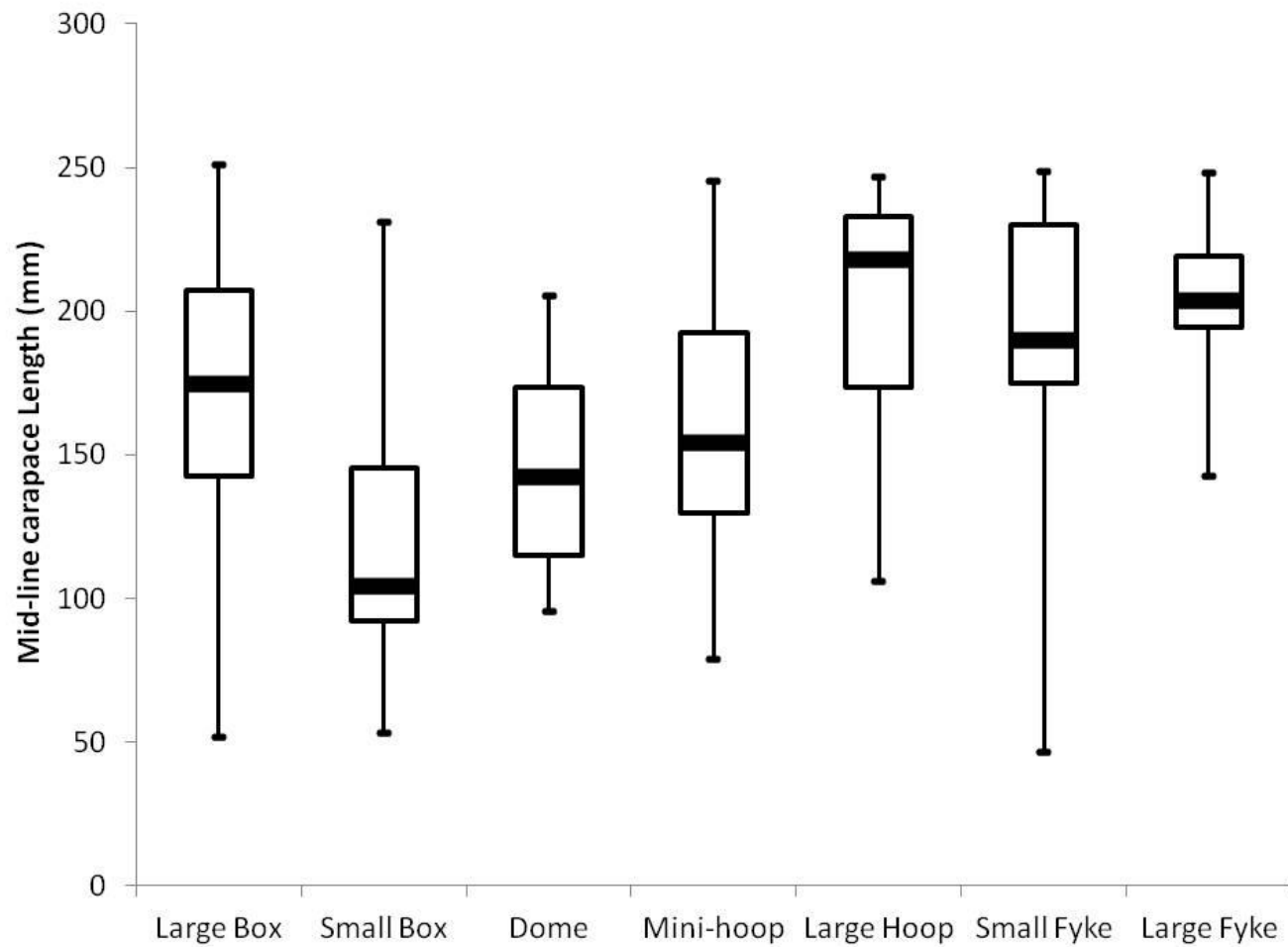


Figure 4.4. Minimum, 1<sup>st</sup> quartile, median, 3<sup>rd</sup> quartile, and maximum mid-line carapace lengths for sliders captured at Gus Engeling WMA, Anderson County, Texas 2006-2009.

Table 4.5: Catch per unit effort x trap type at Keechi Creek Wildlife Management Area, Leon County, Texas 2009.

Trap Type	Net Nights	Total Captures	Species				
			APSP	CHSE	MATE	STCA	TRSC
Large Fyke	4	15	0.00	0.00	0.06	0.13	3.00
Small Fyke	4	11	0.00	0.75	0.00	0.00	2.00
Large Hoop	33	40	0.18	0.03	0.06	0.06	0.87
Large Box	21	28	0.00	0.03	0.00	0.00	1.28
Small Box	16	8	0.00	0.00	0.00	0.00	0.50
All Trap Types	78	92	0.06	0.05	0.03	0.04	0.91

As not all turtles were captured equally in all trap types, sex ratios by trap type include captures from both Gus Engeling WMA and Keechi Creek WMA to provide a more comprehensive picture of captures by sex by net type (Table 4.6). Common musk turtles showed a female bias in all traps in which they were captured. Female common snapping turtles were captured more frequently in small fykes, while males were captured more frequently in large hoop traps. Male pond sliders were captured in trap types with smaller entrances with increasing female captures in larger nets. Pond sliders exhibit sexual size dimorphism, with males being the smaller sex (Ernst and Lovich, 2009), and sex-biased captures are also represented by differences in mean body sizes captured in each trap type (Table 4.6: Fig 4.4).

Table 4.6: Sex ratios (M:F) by species and trap type for Gus Engeling Wildlife Management Area (2006-09) and Keechi Creek Wildlife Management Area (2009). Species abbreviations: CHSE, Common snapping Turtle; KISU, Eastern Mud Turtle; STCA, Razorback Musk Turtle; STOD, Common Musk Turtle; TRSC, Slider.

Trap Type	CHSE	KISU	STCA	STOD	TRSC
Large Fyke				1:1.5	1:2
Small Fyke	1:2	1:1	2:1		1:1
Large Hoop	2:1		1:1.66	1:4	1:1.43
Mini-Hoop			2:1		1:2
Large Box	1:1	1.42:1	1:1		1:1
Small Box					3:1
Dome			1:1		5:1

## Discussion

The sampling techniques I used were adequate for detecting species occurrence with enough sampling effort, as I captured all but one species previously recorded on Gus Engeling WMA (Wes Littrell, Texas Parks and Wildlife Department pers. comm.). The one species missing was the chicken turtle (*Dierochelys reticularia*), which prefer shallow, heavily vegetated bodies of water (Ernst and Lovich, 2009). This habitat type is present at Gus Engeling WMA and was sampled during the study. Based on 4 years of sampling for this project, this species may be extremely rare to extirpated at this site.

River cooters were highly under-represented in my samples, although I observed them basking in open marshy areas quite frequently. 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). Spiny softshells were also underrepresented, and with the exception of one hatchling, all captures of spiny softshell

turtles were female. Ernst and Lovich (2009) suggested that variation in population sizes throughout the spiny softshell's range may be related as much to sampling technique as it is environmental conditions. Spiny softshells typically only make up a low percentage of turtle captures in other studies as well (Bodie *et al.*, 2000; Dreslik *et al.*, 2005; Riedle *et al.*, 2009).

Tinkle (1958) and Trauth *et al.* (2004) commented on low trap success for razorback musk turtles, although I was fairly successful capturing not only razorback musk turtles, but common musk turtles and eastern mud turtles as well. The kinosternids are typically considered bottom walkers (Moll and Moll, 2000; 2004) and the use of fyke nets and box traps may have helped increase our capture success of this family of small turtles. The one advantage box traps had over all other traps was the ability to set them in very shallow water ( $\geq 20$  cm), and in turn they were heavily utilized in backwater and marsh habitats where smaller species and smaller individuals of larger species of turtles may occur.

To properly set large hoop nets, water depth of at least 60 cm was needed, depths generally found in deeper creek habitats. The short length of the trap also allowed me to take advantage of smaller pockets of deeper water that were occasionally present in backwater and marsh habitats. While originally considered deep water gear, fyke nets were more heavily utilized within the shallower backwater habitats (Table 4.1). While successful when set in creek habitats, high flow at certain times of the year made setting the lead on fyke nets difficult within those creeks. Dense aquatic vegetation made setting all types of traps difficult within marsh habitats, particularly during periods of low water.

While sampling effort and community composition differed between Gus Engeling WMA and Keechi Creek WMA, patterns of detectability was similar among trap types and turtle families although overall detectability rates were higher at Keechi Creek WMA (Fig. 4.1). Fyke nets have long been touted as the most efficient way to capture turtles (Vogt, 1980), and even work quite well passively (unbaited) at catching turtles (Webb, 1961; Barko *et al.*, 2004). The long lead off the front frame of fyke nets served to guide turtles towards the opening of the net, and these traps were very successful, particularly for bottom walking species such as the kinosternidae.

Capture rates among sizes and sexes of single species are thought to be biased based upon differences in behavior between sexes and life stages (Cagle and Chaney, 1950). In a Wisconsin population of painted turtles, Ream and Ream (1966) noted higher male captures in baited hoop nets and higher female captures in basking traps. We noted similar discrepancies in sex ratios by trap type for several species (Table 4.4). Most notable was the differentiation between sexes of pond sliders based on the overall size of the trap, with the smaller males being captured more predominantly in smaller traps. A better understanding of sex-biased sampling methods is needed in light of recent research emphases on climatic (Tucker *et al.*, 2008) and ecotoxicological (Willingham and Crews, 1999) impacts on population structure of aquatic turtles.



## CHAPTER V

### CONCLUSIONS

There has been much disagreement about the role of local processes in community ecology (summarized in Ricklefs, 2008; Brooker *et al.*, 2009), but one school of thought is that drivers of local species richness can influence large-scale patterns of community structure (Michalet *et al.*, 2002; Urban *et al.*, 2008).

Understanding how the biotic and abiotic environment at local scales drives local community assemblages has important implications in regards to species conservation and habitat management. Freshwater ecosystems are considered the most endangered in the world (Woodward *et al.*, 2010) with turtles viewed as the most imperiled vertebrate group (Buhlmann *et al.*, 2009). Therefore research on turtle communities and how they are structured can give meaningful insights as to how turtle populations, species, and their aquatic habitats can be managed.

My field research was conducted at two sites in eastern Texas, USA. Catfish Creek is a tributary of the Trinity River in east Texas, is managed by the Texas Parks and Wildlife Department, and is considered a Natural National Landmark (Telfair, 1988). Catfish Creek, and its associated aquatic habitats within the state owned and managed Gus Engeling Wildlife Management Area are manipulated to provide seasonal wetlands for migrating waterfowl. It is important for the area managers to understand how these manipulations impact all the flora and fauna on the area. This project elucidated information on fish and turtle communities on Gus Engeling and Keechi

Creek Wildlife Management Areas in light of these management practices. From a turtle conservation standpoint, my research on turtle communities in Catfish Creek fills some gaps in our knowledge of turtle community structure. Previous literature on riverine turtle communities focus on rivers (Bodie and Semlitsch, 2000; Anderson *et al.*, 2002; Dreslik and Phillips, 2005), with little attention placed on lower-order tributaries.

Fish and turtles can be sampled utilizing the same techniques, and previous but separate works on fish and turtles stated that local species assemblages for both taxa were governed by physical and chemical characteristics of the stream system and interconnectivity among aquatic habitats (Jackson *et al.*, 1992; Luiselli, 2008). All turtles and nearly three-quarters of all fish species were captured along the interface between Catfish Creek and its adjacent backwaters. Although I did not directly measure dispersal between habitats, it appeared that there was interchange between lentic and lotic habitats.

Analyses of stream characteristics showed that outside of flow and emergent vegetation, downed woody debris was an important factor in the determination of species occurrences and abundances. Downed woody debris maintains physical characteristics of stream systems, such as decreasing sediment flux, controlling thermal profile, decreasing bank incision, as well as increasing productivity and diversity of invertebrates (Robertson and Crook, 1999; Brooks *et al.*, 2004). Downed woody debris also provides important cover and/or basking substrate for fish and turtles (Lovich, 1988; Everett and Ruiz, 1993; Lindeman, 1999).

Turtles were the primary focus of my sampling efforts at Gus Engeling Wildlife Management Area in an effort to learn more about assemblage structure, particularly in smaller order streams. Map turtles in the genus *Graptemys*, while present in the regional species pool were absent from this site. Map turtles generally prefer larger streams with more open canopy (Ernst and Lovich, 2009) than was present at Gus Engeling Wildlife Management Area. Other notable differences were the predominance of smaller, subadult alligator snapping turtles. Alligator snapping turtles are typically considered a large river turtle, although juveniles may utilize shallow backwater areas and smaller tributaries (Pritchard, 1989; Ernst and Lovich, 2009). Larger adults are occasionally captured at Gus Engeling Wildlife Management Area and may move up smaller tributaries during periods of high water (Riedle *et al.*, 2006). Based on the capture of one hatchling, some reproduction was apparently taking place on site.

By taking the approach of sampling turtle assemblages, I was also able to elucidate basic information on inter-specific habitat partitioning among closely related groups of turtles. Lescher *et al.* (2013) noted strict habitat partitioning between common and alligator snapping turtles. In his study alligator snapping turtles utilized deeper water and were associated with sites with more submerged structure, while common snapping turtles were associated with sites with more emergent vegetation. At Gus Engeling Wildlife Management Area I observed similar habitat partitioning with alligator snapping turtles captured at sites characterized by deeper water and higher flow, and common snapping turtles were captured at shallower sites.

I also captured three species of kinosternid turtle (common musk turtle, razorback musk turtle, and eastern mud turtle) at Gus Engeling Wildlife Management Area. The Kinosternidae is a vastly understudied group of turtles (Lovich and Ennen, 2013) with the only comparative biology of these three species being published in 1969 (Mahmoud, 1969). On a larger regional scale Mahmoud noted specific habitat preferences among the three species, with eastern mud turtles occurring in more ephemeral habitats and razorback musk turtles being found in lotic habitats. Most notable is that the common musk turtle is considered a habitat generalist and can be found in all habitat types, particularly when it is the only kinosternid occurring in a particular area (Mahmoud, 1969; Ernst and Lovich, 2009). While sampling at a very local scale, this partitioning of habitat was very strong. Differing species of kinosternids were rarely ever captured together at the same sites. Eastern mud turtles were predominantly captured at sites associated with shallow water and dense emergent vegetation. Razorback musk turtles preferred deeper water with high flow. Common musk turtles were then captured in backwaters and smaller streams.

I sampled a second site, Keechi Creek Wildlife Management Area, in 2009 for aquatic turtles. While superficially similar to Gus Engeling Wildlife Management Area, the variety of aquatic habitats available at Keechi Creek Wildlife Management Area was less. In addition it appeared the human perturbations (roads) and potential predators (alligators) were fewer at Keechi Creek Wildlife Management Area. Species richness was less at Keechi Creek Wildlife Management Area, but abundances were higher. Also, individuals tended to be larger at Keechi Creek Wildlife Management Area. While only

two sites were sampled during the course of this study, more extensive sampling of additional sites would provide a tremendous amount of information on how variation in local environment drives turtle assemblage structure.

Sampling a diverse array of turtles ultimately required using a combination of sampling gear. The turtles sampled at Gus Engeling Wildlife Management Area used a variety of aquatic habitats and modes of locomotion ranging from swimming to bottom walking (Moll and Moll, 2000). Using a range of turtle nets that allowed me to adequately sample a range of depths and physical characteristics (lentic vs. lotic) contributed to my overall success of this project. But, two species, river cooters and spiny softshells were underrepresented in my samples at Gus Engeling Wildlife Management Area as they were frequently observed but rarely captured.

Sampling at both Gus Engeling and Keechi Creek Wildlife Management Areas provided valuable information not only on aquatic turtle assemblages, but how turtle assemblages relate to assemblage rule for other aquatic taxa, in this case fish. Expanding this study to include other similar sites throughout the Middle Trinity River Basin would be a big step towards answering many questions on both local drivers of assemblage structure as well as regional level community analyses.

## LITERATURE CITED

- ABBE, T. B., AND D. R. MONTGOMERY. 1996. Large woody debris jams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers: Research and Management* **12**:201-221.
- ALLEN, C. R., E. A. FORYS, K. G. RICE, AND D. P. WOJCIK. 2001. Effects of fire ants (Hymenoptera: Formicidae) on hatchling turtles and prevalence of fire ants on sea turtle nesting beaches in Florida. *Florida Entomologist* 84: 250-253.
- 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.
- ANGERMEIER, P. L., AND J. R. KARR. 1984. Relationships between debris and fish habitat in a small warmwater stream. *Transactions of the American Fisheries Society* **113**:716-726.
- ARESCO, M. J. AND M.S. GUNZBURGER. 2007. Ecology and morphology of *Chelydra serpentina* in northwestern Florida. *Southeastern Naturalist* **6**:435-448.
- BARKO, V. A., AND J. T. BRIGGLER. 2006. Midland smooth softshell (*Apalone mutica*) and spiny softshell (*Apalone spinifera*) turtles in the middle Mississippi River: Habitat associations, population structure, and implications for conservation. *Chelonian Conservation and Biology* **5**:225-231.
- BARKO, V. A., J. T. BRIGGLER, AND D. E. OSTENDORF. 2004. Passive fishing techniques: A cause of turtle mortality in the Mississippi River. *Journal of Wildlife Management* **68**:1145-1150.
- BASS, A. A. 2007. Habitat use and movements of alligator snapping turtle (*Macrochelys*

- temminckii*) hatchlings. Unpublished MS Thesis, University of Louisiana, Monroe.
- BAYLEY, P. B. 1995. Understanding large river floodplain ecosystems. *Bioscience* **45**:153-158.
- 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.
- BONDAVALLI, C., AND R. E. ULANOWICZ. 1999. Unexpected effects of predators upon their prey: the case of the American alligator. *Ecosystems* **2**:49-63.
- BROOKER, R.W., R.M. CALLAWAY, L.A. CAVIERES, Z. KIKVIDZE, C.J. LORTIE, R. MICHALET, F.I. PUGNAIRE, A. VALIENTE-BANUET, AND T.G. WHITHAM. 2009. Don't diss integration: a comment on Ricklefs's disintegrating communities. *The American Naturalist* **174**:919-927.
- BROOKS, A. P., P. C. GEHRKE, J. D. JANSEN, AND T. B. ABBE. 2004. Experimental reintroduction of woody debris on the Williams River, NSW: geomorphic and ecological responses. *River Research and Applications* **20**:513-536.
- BROWNE, C. L., AND S. J. HECNAR. 2007. Species loss and shifting population structure of freshwater turtles despite habitat protection. *Biological Conservation* **138**:421-429.
- BUHLMANN, K. A., T. S. B. AKRE, J. B. IVERSON, D. KARAPATAKIS, R. A. 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 G. COFFMAN. 2001. Fire ant predation of turtle nests and implications for the strategy of delayed emergence. *The Journal of the Elisha Mitchell Scientific Society* **117**:94-100.
- 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.
- BURY, B. R. 1979. Population ecology of freshwater turtles, p. 571-602. *In*: Harless, M and H. Morlock (eds.). *Turtles: Perspectives and Research*. Krieger Publishing Company, FL, USA.
- CAGLE, F. R., 1942. Turtle populations in southern Illinois. *Copeia* **1942**:155-162.
- CAGLE, F. R., 1950. The life history of the slider turtle *Pseudemys scripta* troostii (Holbrook). *Ecological Monographs* **20**:31-54.
- CAGLE, F. R., AND A. H. CHANEY. 1950. Turtle populations in Louisiana. *The American Midland Naturalist* **43**:383-388.
- CHANEY, A., AND C. L. SMITH. 1950. Methods for collecting map turtles. *Copeia* **1950**:323-333
- CHAPIN, F. S., E. S. ZAVALA, V. T. EVINER, R. L. NAYLOR, P. M. VITOUSEK, H. L. REYNOLDS, D. U. HOOPER, S. LAVOREL, O. S. SALA, S. E. HOBBI, M. C. MACK, S. DIAZ. 2000. Consequences of changing biodiversity. *Nature* **405**:234-242.



- CHASE, J. M., AND M. A. LEIBOLD. 2003. Ecological Niches. University of Chicago Press, Chicago.
- CHESSON, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**:343-366.
- CHIARUCCI, A., G. BACARO, D. ROCCHINI, AND L. FATTORINI. 2008. Discovering and rediscovering the sample-based rarefaction formula in the ecological literature. *Community Ecology* **9**:121-123.
- CLARK, D. B., and J. W. GIBBONS. 1969. Dietary shift in the turtle *Pseudemys scripta* (Schoepff) from youth to maturity. *Copeia* **1969**:704-706.
- COLWELL, R.K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- COLWELL, R.K., A. CHAO, N.J. GOTELLI, S.-Y. LIN, C.X. MAO, R.L. CHAZDON, AND J.T. LONGINO. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. *Journal of Plant Ecology* **5**:3-12.
- CONGDON, J.D., J.L. GREENE, AND J.W. GIBBONS. 1986. Biomass of freshwater turtles: a geographic comparison. *American Midland Naturalist* **115**:165-173.
- CONNOR, E.F., AND D. SIMBERLOFF. 1979. The assembly of species communities: chance or competition. *Ecology* **60**:1132-1140.
- CORN, P.S., E. MUTHS, AND W.M. IKO. 2000. A comparison in Colorado of three methods to monitor breeding amphibians. *Northwestern Naturalist* **81**:22-30.

- 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.
- DECAMPS, H. 1993. River margins and environmental change. *Ecological Applications* **3**:441-445.
- DEITZ, D. C., AND D. R. JACKSON. 1979. Use of American alligator nests by nesting turtles. *Journal of Herpetology* **13**:510-12.
- DIAMOND, J. M. 1975. Assembly of species communities, p. 342-444. *In*: Cody, M. L., and J. M. Diamond (eds.). Ecology and evolution of communities. Harvard University Press, Cambridge, MA.
- 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.
- DOUPE, R. G., J. SCHAFFER, M. J. KNOTT, AND P. W. DICKY. 2009. A description of freshwater turtle habitat destruction by feral pigs in tropical north-eastern Australia. *Herpetological Conservation and Biology* **4**:331-339.
- DRESLIK, M. J., A. R. KUHN, AND C. A. PHILLIPS. 2005. Structure and composition of a southern Illinois freshwater turtle assemblage. *Northeastern Naturalist* **12**:173-186.
- DRESLIK, M. J. AND C. A. PHILLIPS. 2005. Turtle communities in the Upper Midwest, USA. *Journal of Freshwater Ecology* **20**:149-164.
- DUNNING, J. B., B. J. DANIELSON, AND H. R. PULLIAM. 1992. Ecological processes that

- affect populations in complex landscapes. *Oikos* **65**:169-175.
- ECHELLE, A. A., AND C. D. RIGGS. 1972. Aspects of the early life histories of gars (*Lepisosteus*) in Lake Texoma. *Transactions of the American Fisheries Society* **101**:106-112.
- EDDS, D. R. 1993. Fish assemblage structure and environmental correlates in Nepal's Gandaki River. *Copeia* **1993**:48-60.
- ERNEST, S. K., J. H. BROWN, K. M. THIBAUT, E. P. WHITE, AND J. R. GOHEEN. 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. *The American Naturalist* **172**: 257-269.
- ERNST, C. H. 1965. Bait preferences of some freshwater turtles. *Ohio Herpetological Society Newsletter* **5**:53.
- ERNST, C. H., AND J. E. LOVICH. 2009. Turtles of the United States and Canada. The John Hopkins University Press, Baltimore, MA.
- ETNIER, D. A., AND W. C. STARNES. 1993. The Fishes of Tennessee. The University of Tennessee Press, Knoxville.
- EVERETT, R. A., AND G. M. RUIZ. 1993. Coarse woody debris as a refuge from predation in aquatic communities. *Oecologia* **93**:475-486.
- EWERT, M. A., D. R. JACKSON, AND P. E. MOLER. 2006. *Macrochelys temminckii*—Alligator snapping turtle, p. 58-71 In Meylan, P. A. (ed). Biology and Conservation of Florida Turtles. Chelonian Research Monograph 3: 58-71.
- 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.
- FORDHAM, D., A. GEORGES, B. COREY, AND B. W. BROOK. 2006. Feral pig predation threatens the indigenous harvest and local persistence of snake-necked turtles in northern Australia. *Biological Conservation* **133**:379-388.
- FUASCH, K. D., C. E. TORGERSEN, C. V. BAXTER, AND W. L. HIRAM. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience* **52**:483-498.
- FUSELIER, L., AND D. EDDS. 1994. Habitat partitioning among three sympatric species of map turtles, genus *Graptemys*. *Journal of Herpetology* **28**:154-158.
- GALAT, D. L., L. H. FREDRICKSON, D. D. HUMBURG, K. J. BATAILLE, J. R. BODIE, J. DOHRENWEND, G. T. GELWICKS, J. E. HAVEL, D. L. HELMERS, J. B. HOOKER, J. R. JONES, M. F. KNOWLTON, J. KUBISIAK, J. MAZOUREK, A. C. MCCOLPIN, RENKEN, R. B., AND R. D. SEMLITSCH. 1998. Flooding to restore connectivity of regulated, large river wetlands. *Bioscience* **48**:721-733.
- GEHRT, S. D., G. F., HUBERT, AND J. A. ELLIS. 2002. Long-term population trends of raccoons in Illinois. *Wildlife Society Bulletin* **30**:457-463.
- GELWICK, F. P., B. D. HEALY, N. J. DICTSON, AND R. KNIPE. 2001. Fishes of the Keechi Creek Wildlife Management Area of East Texas. *The Texas Journal of Science* **53**:13-18.
- GIBBONS, J. W. 1990. Sex ratios and their significance among turtle populations, p. 171-

182. *In*: J. W. Gibbons (ed.). Life history and ecology of the slider turtle. Smithsonian Institution Press, Washington, D.C.
- GIBBONS, J. W., AND J. E. LOVICH. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs* **1990**:1-29.
- GIBBONS, J. W., D. E. SCOTT, T. J. RYAN, K. A. BUHLMANN, T. D. TUBERVILLE, B. S. METTS, J. L. GREENE, T. MILLS, Y. LEIDEN, S. POPPY, AND C. T. WINNE. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* **50**:653-665.
- GIBBS, J. P., AND D. A. STEEN. 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. *Conservation Biology* **19**:552-556.
- GORMAN, O.T., AND J. R. KARR. 1978. Habitat structure and stream fish communities. *Ecology* **60**:507-515.
- GOTELLI, N.J. AND R. K. COLWELL. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**:379-391.
- GOTELLI, N. J., AND G. L. ENTSMINGER. 2001. EcoSim: null models software for ecology. Version 7.0. Acquired Intelligence Inc. and Kesey-Bear, Montrose CO.
- GROSSMAN, G. D. 1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. *American Naturalist* **119**:611-637.
- GROSSMAN, G.D., P. B. MOYLE, AND J. O. WHITAKER JR. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: A test of community theory. *The American Naturalist* **120**:423-454.

- GUNZBURGER, M.S. 2007. Evaluation of seven aquatic sampling methods for amphibians and other aquatic fauna. *Applied Herpetology* **4**:47-63.
- HART, D. D. 1992. Community organization in streams: the importance of species interactions, physical factors, and change. *Oecologia* **91**:220-228.
- HELLGREN, E. C., R. T. KAZMAIER, D. C. RUTHVEN III, AND D. R. SYNATZSKE. 2000. Variation in tortoise life history: demography of *Gopherus berlandieri*. *Ecology* **8**:1297-1310.
- HEYER, W. R., M. A. DONNELLY, R. W. MCDIARMID, L. C. HAYEK, AND M. S. FOSTER. 1994. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, D. C.
- HINES, J.E. 2006. PRESENCE2 – Software to estimate patch occupancy and related parameters. USGS-PWRC.  
<http://www.mbrpwrc.usgs.gov/software/presence.html>
- HUBBELL, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.
- HUGHES, R. M., L. WANG, AND P. W. SEELBACH. 2006. Landscape Influences on Stream Habitats and Biological Assemblages. American Fisheries Society, Bethesda, MD.
- HUSER, V. 2001. Rivers of Texas. Texas A&M University Press, College Station, TX.
- IVERSON, J.B. 1982. Biomass in turtle populations: a neglected subject. *Oecologia* **55**:69-76.

- IVERSON, J. B. 1992. Global correlates of species richness in turtles. *The Herpetological Journal* **2**:77-81.
- IVERSON, J. B. 2002. Reproduction in female razorback musk turtles (*Sternotherus carinatus*: Kinosternidae). *The Southwestern Naturalist* **47**:215-224.
- JACKSON, D. A., AND H. H. HARVEY. 1989. Biogeographic associations in fish assemblages: local vs. regional processes. *Ecology* **70**:1472-1484.
- JACKSON, D. A., P. R. PERES-NETO, AND J. D. OLDEN. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Science* **58**:157-170.
- JACKSON, D. A., K. M. SOMERS, AND H. H. HARVEY. 1992. Null models and fish communities: Evidence of nonrandom patterns. *The American Naturalist* **139**:930-951.
- JENSEN, J. B., AND W. S. BIRKHEAD. 2003. Distribution and status of the alligator snapping turtle (*Macrochelys temminckii*) in Georgia. *Southeastern Naturalist* **2**:25-34.
- JOHANSEN, K., D. HANSON, AND C. LENFANT. 1970. Respiration in a primitive air breather, *Amia calva*. *Respiration Physiology* **9**:162-174.
- JOHNSON, B. L., W. B. RICHARDSON, AND T. J. NAIME. 1995. Past, present, and future concepts in large river ecology. *Bioscience* **45**:134-141.
- JOHNSON, E. H. 1931. The Natural Regions of Texas. The University of Texas Bulletin No. 3113, Bureau of Business Research Monograph No. 8.
- JUNK, W. J., P. B. BAYLEY, AND R. E. SPARKS. 1989. The flood pulse concept in river-

- floodplain systems, p. 110-127 *In*: D. P. Dodge (ed). Proceedings of the International Large River Symposium. Canadian Special Publications in Fishery and Aquatic Science 106.
- KLEMENS, M. W. 2000. Turtle Conservation. Smithsonian Institution Press, Washington D.C.
- KOPER, N., AND R. J. BROOKS. 1998. Population size estimators and unequal catchability in painted turtles. *Canadian Journal of Zoology* **76**:458-465.
- LAGLER, K. F. 1943. Methods of collecting freshwater turtles. *Copeia* **1943**:21-25.
- LAKE, P.S., M.A. PALMER, P. BIRO, J. COLE, A.P. COVICH, C. DAHM, J. GIBERT, W. GOEDKOOP, K. MARTENS, AND J. VERHOEVEN. 2000. Global change and the biodiversity of freshwater ecosystems: impacts on linkages between above-sediment and sediment biota. *BioScience* **50**:1099-1107.
- LAMBACK, R.J. 1997. Focal Species: a multi-species umbrella for nature conservation. *Conservation Biology* **11**:849-856.
- LANDHOLT, L. M. AND H. H. GENOWAYS. 2000. Population trends in furbearers in Nebraska. *Transactions of the Nebraska Academy of Sciences* **26**:97-110.
- LAWTON, J.H. 1999. Are there general laws in ecology? *Oikos* **84**:177-192.
- LEIBOLD, M. A., M. HOLYOAK, N. MOUQUET, P. AMARASEKARE, J. M. CHASE, M. F. HOOPES, R. D. HOLT, J. B. SHURIN, R. LAW, D. TILMAN, M. LOREAU, AND A. GONZALEZ. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**:601-613.
- 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. 1999. Surveys of basking map turtles *Graptemys* spp. In three river drainages and the importance of deadwood abundance. *Biological Conservation* **88**:33-42.
- 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. 2008. *Sternotherus carinatus* Gray 1856 — razor back musk turtle, razor-backed musk turtle. P. 012.1-012.6. In: Rhodin, A. G. J., P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, and J. B. Iverson (eds.). *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. Chelonian Research Monographs No. 5
- 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.

- LONGINO, J.T., AND R.K. COLWELL. 2011. Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere* **23**:art29.  
doi:10.1890/ES10-00200.1
- LOSOS, J. B. 1996. Phylogenetic perspectives on community ecology. *Ecology* **77**:1344-1354.
- LOVICH, J. 1988. Aggressive basking behavior in eastern painted turtles (*Chrysemys picta picta*). *Herpetologica* **44**:197-202.
- LOVICH, J.E. AND J.R. ENNEN. 2013. A quantitative analysis of the state of knowledge of turtles of the United States and Canada. Amphibia-Reptilia  
DOI:10.1163/15685381-00002860.
- LUISELLI, L. 2008. Resource portioning in freshwater turtle communities: a null model meta-analysis of available data. *Acta Oecologica* **34**:80-88.
- MAGURRAN, A. E. 2004. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.
- MAHMOUD, I. Y. 1969. Comparative ecology of the Kinosternid turtles of Oklahoma. *The Southwestern Naturalist* **14**:31-66.
- MARCHAND, L. J. 1945. Water goggling: a new method for the study of turtles. *Copeia* **1945**:37-40.
- MATTHEWS, W. J., AND L. G. HILL. 1980. Habitat partitioning in the fish community of a southwestern river. *The Southwestern Naturalist* **25**:51-66.
- MATTHEWS, W. J., AND J. T. STYRON JR. 1981. Tolerance of headwater vs. mainstream fishes for abrupt physiochemical changes. *American Midland Naturalist*

**105**:149-158.

- MCGOWAN, J. A., AND P. A. WALKER. 1993. Pelagic diversity patterns, p. 203-214 *In*: Ricklefs, R. E., and Schluter, D. (eds.). Species diversity in ecological communities. University of Chicago Press, Chicago, IL.
- MEFFE, G. K., AND A. L. SHELDON. 1988. The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. *American Midland Naturalist* **120**:225-240.
- MICHALET, R., C. GANDOY, D. JOUD, J.P. PAGES, AND P. CHOLER. 2002. Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: comparative effects of soil chemistry and water status. *Arctic, Antarctic, and Alpine Research* **34**:102-113.
- MICHENER, W. K., AND R. A. HAEUBER. 1998. Flooding: Natural and managed disturbances. *Bioscience* **48**:677-680.
- MITCHELL, J. C. 1988. Population ecology and life histories of the freshwater turtles *Chrysemys picta* and *Sternotherus odoratus* in an urban lake. *Herpetological Monographs* **2**:40-61.
- MITCHELL, J. C., AND M. W. KLEMENS. 2000. Primary and secondary effects of habitat alteration, p. 5-32 *In*: Klemens, M. W. (ed.). Turtle Conservation. Smithsonian Institution Press, Washington D.C.
- MOLL, D. 1976. Food and feeding strategies of the Ouachita map turtle (*Graptemys pseudogeographica ouachitensis*). *American Midland Naturalist* **96**:478-482.

- MOLL, D. 1990. Population sizes and foraging ecology in a tropical freshwater stream turtle community. *Journal of Herpetology* **24**:48-53.
- MOLL, D., AND E. O. MOLL. 2004. The Ecology, Exploitation, and Conservation of River Turtles. Oxford University Press, New York.
- MOLL, E. O., AND D. MOLL. 2000. Conservation of river turtles. p. 126-155. *In*: Klemens, M.W. (ed.). Turtle Conservation. Smithsonian Institution Press, Washington, D. C.
- MONTGOMERY, D. R. 1999. Process domains and the river continuum concept. *Journal of the American Water Resources Association* **35**:397-410.
- MOULIS, R. A. 1997. Predation by imported fire ant (*Solenopsis invicta*) on loggerhead sea turtle (*Caretta caretta*) nests on Wassaw National Wildlife Refuge, Georgia. *Chelonian Conservation and Biology* **10**:570-577.
- NAIMAN, R. J., R. E. BILBY, D. E. SCHINDLER, AND J. M. HELFIELD. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* **5**:399-417.
- NAIMAN, R. J., AND K. H. ROGERS. 1997. Large animals and system-level characteristics in river corridors. *Bioscience* **47**:521-529.
- NATURAL RESOURCES CONSERVATION SERVICE. 2003. Fish assemblages as indicators of the biological condition of streams and watersheds. Wetland Science Institute Technical Note. Laurel, MD, USA.
- PAINE, R. T. 1974. Intertidal community structure: experimental studies between a dominant competitor and its principal predator. *Oecologia* **15**:93-120.

- PAINE, R. T. 1976. Size limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57**:858-873.
- PALMER, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* **74**:2215-2230.
- PATRICK, R., AND D. M. PALAVAGE. 1994. The value of species as indicators of water quality. *Proceedings of the Academy of Natural Sciences of Philadelphia* **145**:55-92.
- PIANKA, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* **4**:737-741.
- PLUMMER, M.V. 1979. Collecting and Marking. Pp. 45-60 *In* Turtles: Perspectives and Research. Harless, M., and H. Morlock (Eds.). John wiley & Sons, Inc., new York, New York, USA.
- POOLE, G. C. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology* **47**:641-660.
- PRENTICE, H. C., AND W. CRAMER. 1990. The plant community as a niche bioassay: environmental correlates of local variation in *Gypsophila fastigiata*. *Journal of Ecology* **78**:313-325.
- PRESSEY, R.L., M. CABEZA, M.E. WATTS, R.M. COWLING, AND K.A. WILSON. 2007. Conservation planning in a changing world. *Trends in Ecology and Evolution* **22**:583-592.
- PRINGLE, C. M., R. J. NAIMAN, G. BRETSCHKO, J. R. KARR, M. W. OSWOOD, J. R.

- WEBSTER, R. L. WELCOMME, AND M. J. WINTERBOURN. 1988. Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society* **7**:503-524.
- PRITCHARD, P. C. H. 1989. The alligator snapping turtle: Biology and conservation. Milwaukee Public Museum, Milwaukee, WI, USA.
- R DEVELOPMENT CORE TEAM. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.  
<http://www.R-project.org>.
- 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.
- RICKLEFS, R. E. 1987. Community diversity: Relative roles of local and regional processes. *Science* **235**:167-171.
- RICKLEFS, R. E., AND D. SCHLUTER. 1993. Species diversity: regional and historical influences, p. 351-363 *In*: Ricklefs, R. E., and D. Schluter (eds.). Species diversity in ecological communities. University of Chicago Press, Chicago, IL.
- RIEDLE, J. D., P. A. SHIPMAN, S. F. FOX, AND D. M. LESLIE. 2005. Status and distribution of the alligator snapping turtle, *Macrochelys temminckii*, in Oklahoma. *The Southwestern Naturalist* **50**:79-84.
- 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. *The 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.
- RINNE, J. N., R. M. HUGHES, AND B. CALAMUSSO. 2005. Historical changes in large river fish assemblages of the Americas. American Fisheries Society, Symposium 45, Bethesda, Maryland.
- RISLEY, P. L. 1933. Observations on the natural history of the common musk turtle, *Sternotherus odoratus* (Latreille). *Papers of the Michigan Academy of Science, Arts, and Letters* **17**:685-711.
- ROBERTSON, A. I., AND D. A. CROOK. 1999. Relationships between riverine fish and woody debris: implications for lowland rivers. *Marine and Freshwater Research* **50**:941-953.
- ROBISON, H. W., AND T. M. BUCHANAN. 1988. Fishes of Arkansas. University of Arkansas Press, Fayetteville.
- RUTHVEN, A. G. 1912. Directions for collecting and preserving specimens of reptiles and amphibians for museum purposes. *14<sup>th</sup> Annual Report of the Michigan Academy of Science*:165-176.
- RYBERG, W. A., L. A. FITZGERALD, R. L. HONEYCUTT, J. C. CATHEY, AND T. J. HIBBITTS. 2004. Vertebrate inventory of Richland Creek Wildlife Management Area in eastern Texas. *The Southwestern Naturalist* **49**:528-534.
- SALA, O. E., F. S. CHAPIN, J. J. ARMESTO, R. BERLOW, J. BLOOMFIELD, R. DIRZO, E. HUBER-SANWALD, L. F. HUENNEKE, R. B. JACKSON, A. KINZIG, R. LEEMANS, D. LODGE, H. A. MOONEY, M. OESTERHELD, N. L. POFF, M. T. SYKES, B. H.

- WALKER, M. WALKER, AND D. H. WALL. 2000. Global diversity scenarios for the year 2100. *Science* **287**:1770-1774.
- SALE, P. F. 1980. Assemblages of fish on patch reefs – predictable or unpredictable? *Environmental Biology of Fishes* **5**:243-249.
- SANDERSON, E.W., K.H. REDFORD, A. VEDDER, P.B. COPPOLILLO, S. E. WARD. 2002. A conceptual model for conservation planning based on landscape species requirements. *Landscape and Urban Planning* **58**:41-56.
- SCHLOSSER, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* **41**:704-712.
- SCHLOSSER, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* **303**:71-81.
- SCHMIDLY, D. J. 1983. Texas mammals east of the Balcones Fault Zone. Texas A&M University Press, College Station, TX.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* **185**:27-39.
- SCOTT, N. J. 1982. Herpetological communities. United States Fish and Wildlife Service Wildlife Research Report 13. Washington, D. C.
- SEMLITSCH, R. D., AND J. R. BODIE. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* **17**:1219-1228.
- SHIPMAN, P. A., D. EDDS, AND D. BLEX. 1994. *Macrolemmys temminckii* (alligator



- snapping turtle) and *Chelydra serpentina* (common snapping turtle): agnostic behavior. *Herpetological Review* **25**:24-25.
- SHIPMAN, P. A., AND J. D. RIEDLE. 2008. Status and distribution of the alligator snapping turtle (*Macrochelys temminckii*) in southeastern Missouri. *Southeastern Naturalist* **7**:331-338.
- SLOAN, K. N., AND D. TAYLOR. 1987. Habitats and movements of adult alligator snapping turtles in northeast Louisiana. *Proceedings of the annual conference of Southeastern Association of Fish and Wildlife Agencies* **41**:343-348.
- SMITH, G. R., AND J. B. IVERSON. 2002. Sex ratio of common musk turtles (*Sternotherus odoratus*) in a north-central Indiana lake: a long-term study. *American Midland Naturalist* **148**:185-189.
- SMITH, N. J. H. 1979. Aquatic turtles of Amazonia: an endangered resource. *Biological Conservation* **16**:165-176.
- STEPHENS, P. R., AND J. J. WEINS. 2003. Explaining species richness from continents to communities: The time for speciation effect in Emydid turtles. *The 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. *The American Naturalist* **164**:244-254.
- STERRETT, S. C., L. L. SMITH, S. H. SCHWEITZER, AND J. C. MAERZ. 2010. An assessment of two methods for sampling river turtle assemblages. *Herpetological Conservation and Biology* **5**:490-497.

- STONE, P. A., AND J. B. IVERSON. 1999. Cutaneous surface area in freshwater turtles. *Chelonian Conservation and Biology* **3**:512-515.
- SUBALUSKY, A. L., L. A. FITZGERALD, AND L. L. SMITH. 2009. Ontogenetic niche shifts in the American alligator establish functional connectivity between aquatic systems. *Biological Conservation* **142**:1507-1514.
- TAYLOR, C. M. 1997. Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. *Oecologia* **110**:560-566.
- TAYLOR, C. M., AND M. L. WARREN. 2001. Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology* **82**:2320-2330.
- TELFAIR, R. C. 1988. Conservation of the Catfish Creek ecosystem: a national natural landmark in eastern Texas. *The Texas Journal of Science* **40**:11-23.
- 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 A. P. SCHAFFERS. 2004. Co-correspondence analysis: a new ordination method to relate two community compositions. *Ecology* **85**:834-846.
- 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.
- TILMAN, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences* **101**:10854-10861.
- TINKLE, D. W. 1958. The systematics and ecology of the *Sternotherus carinatus* complex (Testudinata: Chelydridae). *Tulane Studies in Zoology* **6**:3-56.
- TINKLE, D. W. 1959. The relation of the fall line to the distribution and abundance of turtles. *Copeia* **1952**:167-170.
- TINKLE, D. W. 1961. Geographic variation in reproductive size, sex ratio, and maturity of *Sternotherus odoratus* (Testudinata: Chelydridae). *Ecology* **42**:68-76.
- TOWNSEND, C. R. 1989. The patch dynamics concept of stream ecology. *Journal of the North American Benthological Society* **8**:36-50.
- TRAUTH, S. E., H. W. ROBISON, AND M. V. PLUMMER. 2004. The amphibians and reptiles of Arkansas. The University of Arkansas Press, Fayetteville, USA.
- TRAUTH, S. E., J. D. WILHIDE, AND A. HOLT. 1998. Population structure and movement patterns of alligator snapping turtles (*Macrolemys temminckii*) in northeastern Arkansas. *Chelonian Conservation and Biology* **3**:64-70.
- TUCKER, J.K., C.R. DOLAN, J.T. LAMER, AND E. A. DUSTMAN. 2008. Climatic warming, sex ratios, and red-eared sliders (*Trachemys scripta elegans*) in Illinois. *Chelonian Conservation and Biology* **7**:60-69.
- URBAN, M.C., M.A. LEIBOLD, P. AMARASEKARE, L. MEESTER, R. GOMULKIEWICZ, M.E.

- HOCHBERG, C.A. KLAUSMEIER, N. LOEUILLE, C. DE MAZANCOURT, J. NORBERG, J.H. PANTEL, S.Y. STRAUSS, M. VELLEND, AND M.J. WADE. 2008. The evolutionary ecology of metacommunities. *Trends in Ecology and Evolution* **23**:311-317.
- 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.
- VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:130-137.
- VELLEND, M. 2010. Conceptual synthesis in community ecology. *The Quarterly Review of Biology* **85**:183-205.
- VOGT, R. C. 1980. New methods for trapping aquatic turtles. *Copeia* **1980**:368-371.
- VOGT, R. C., AND S. GUZMAN-GUZMAN. 1988. Food portioning in a Neotropical turtle community. *Copeia* **1988**:37-47.
- VOORHEES, W., J. SCHNELL, AND D. EDDS. 1991. Bait preferences of semi-aquatic turtles in southeast Kansas. *Kansas Herpetological Society Newsletter* **85**:13-15.
- WANG, L., P. W. SEELBACH, AND R. M HUGHES. 2006. Introduction to landscape influences on stream habitats and biological assemblages, p. 1-23 *In*: R. W. Hughes, L. Wang, and P. W. Seelbach (eds.). *Landscape Influences on Stream Habitats and Biological Assemblages*. American Fisheries Society, Bethesda, MA.

- WEBB, R.G. 1961. Observations on the life histories of turtles (genus *Pseudemys* and *Graptemys*) in Lake Texoma. *American Midland Naturalist* **65**:193-214.
- WELCOMME, R. L. 1979. Fisheries ecology of floodplain rivers. Longman Group, New York.
- WELLS, K. D. 2007. The ecology and behavior of amphibians. The University of Chicago Press, Chicago, IL.
- WELTY, J. J., T. BEECHIE, K. SULLIVAN, D. M. HYINK, R. E. BILBY, C. ANDRUS, AND G. PRESS. 2002. Riparian aquatic interaction simulator (RAIS): a model of riparian forest dynamics for the generation of large woody debris and shade. *Forest Ecology and Management* **162**:299-318.
- WHITMAN, R. L., AND W. J. CLARK. 1984. Ecological studies of the sand-dwelling community of an east Texas stream. *Freshwater Invertebrate Biology* **3**:59-79.
- WILKINSON, C. D., AND D. R. EDDS. 2001. Spatial pattern and environmental correlates of a midwestern stream fish community: including spatial autocorrelation as a factor in community analyses. *The American Midland Naturalist* **146**: 271-289.
- WILLINGHAM, E., AND D. CREWS. 1999. Sex reversal effects of environmentally relevant xenobiotic concentrations on the red-eared slider turtles, a species with temperature dependent sex determination. *General and Comparative Endocrinology* **113**:429-435.
- WINEMILLER, K. O., A. S. FLECKER, AND D. J. HOEINGHAUS. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* **29**:84-99.

- WINEMILLER, K. O., S. TARIM, D. SHORMANN, AND J. B. COTNER. 2000. Fish assemblage structure in relation to environmental variation among Brazos River oxbow lakes. *Transactions of the American Fisheries Society* **129**:451-468.
- WOODWARD, G., D.M. PERKINS, AND L.E. BROWN. 2010. Climate Change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society* **365**:2093-2106.