

FRESHWATER RIVER TURTLE POPULATIONS INFLUENCED BY A NATURALLY
GENERATED THERMAL GRADIENT

By

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To my father,
Albert L. Pitt, Sr.,
for showing me the wonders of rivers

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LIST OF ABBREVIATIONS

CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
DF	Degrees of freedom
IUCN	International Union for the Conservation of Nature and Natural Resources
MDNR	Missouri Department of Natural Resources
MPN	Most probable number of colony-forming units per 100 ml of water
NFWR	North Fork of White River
NOAA	National Oceanic and Atmospheric Administration
USFWS	United States Fish and Wildlife Service

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By

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The North Fork of White River (NFWR), Ozark County, Missouri, receives a large volume of water from several major springs. These springs create a temperature gradient along the stream's length. Historical studies dating back to 1969 of a 4.6 km section of NFWR reveal that the North Fork supports a diverse turtle community, predominated by the northern map turtle (*Graptemys geographica*). The 4.6 km research section from which historical data are available is located downstream of the major spring-flows and thus represents a relatively cooler portion of the stream for much of the year, but especially during the summer months. Because rivers, especially those that are spring-fed, such as NFWR, are spatially and temporally dynamic, it was hypothesized that turtle communities may differ within various sections of the same river. Additionally, because temperature can influence turtles' physiology, it was hypothesized that turtles in the upstream, and therefore relatively warmer, sections of NFWR, may grow faster than those in areas downstream of the major spring-flows.

Assessment of turtle populations and communities located in thermally distinct areas of NFWR indicated that community composition differed within relatively close sections of the same river. Furthermore, the turtle community located in a less impacted (by humans) section of NFWR more closely resembled the community described in 1969 surveys in an area that is now

degraded. These results indicated that thermal regimes, habitat quality, and microhabitat availability influence chelonian community composition.

Significant temperature differences within NFWR did not appear to influence turtle growth rate, though body temperature and behavior of *G. geographica* varied with thermal habitat. Growth rate did vary with time and length of growing season. These patterns indicate that global climate change may influence turtle growth rate. Von Bertalanffy growth curves were generated for male and female *G. geographica* inhabiting NFWR, thus providing information relevant to life history characteristics that can be compared with data from other populations or taxa.

CHAPTER 1 INTRODUCTION

Background

There is a general consensus that many turtle populations are declining worldwide (Smith 1979, Moll 1986, Kuchling 1988, Ernst et al. 1994, Buhlmann and Gibbons 1997, Gibbons 1997, Haitao 2000, van Dijk et al. 2000) although many species, especially those considered “common” (Dodd and Franz 1993:47), lack sufficient population data to support this claim (Congdon et al. 1993, Dodd and Franz 1993, Dreslik 1998, Moll and Moll 2004). River turtles in particular are largely ignored by researchers and receive little public support for conservation (Moll and Moll 2004) though numerous threats to populations exist, including exploitation, pollution, disease, and habitat degradation, fragmentation and destruction (Ernst et al. 1994, Buhlmann and Gibbons 1997, Jacobson 1997, Kannan et al. 2000, Moll and Moll 2004).

Turtle conservation is essential for maintaining river ecosystems. Turtles are a major biomass component of river communities and connect the aquatic and terrestrial environments, bolstering nutrient cycling and energy flow (Congdon et al. 1986, Moll and Moll 2004). They maintain critical links in the food web as predators and scavengers (Moll and Moll 2004). Turtles at all life stages are important prey for terrestrial and semi-aquatic vertebrates such as foxes, raccoons, and otters, and for invertebrates such as fly larvae (Vogt 1981b, Cochran 1987, Moll and Moll 2004). Turtles may also be important for their roles in interspecific mutualisms (Vogt 1979). For example, basking map turtles (*Graptemys* spp.) benefit from removal of leeches by common grackles (*Quiscalus quiscula*) (Vogt 1979). In turn, grackles benefit from the sedentary, protein-rich food source (Vogt 1979). The ecological ramifications of declines of certain species are unknown (Sutherland 1974, Iverson 1992), yet the impending loss of biomass,

diminished nutrient cycling and energy flow, and simplification of food webs associated with turtle declines have the potential to create substantial changes in an ecosystem.

Conservation of turtle species is impeded by the dearth of essential population and community data (Ernst et al. 1994, Moll and Moll 2004). This shortage of information is largely due to the sheer nature of collecting it. Accurate assessment of turtle population status requires long-term studies on the scale of decades to account for life history characteristics such as long-life and delayed sexual maturation (Congdon et al. 1993, Congdon et al. 1994, Foscarini and Brooks 1997). These same life history characteristics do not permit reduced populations to rebound from chronic disturbances, furthering the propensity for decline (Congdon and Gibbons 1990, Congdon et al. 1993, Congdon et al. 1994, Buhlmann and Gibbons 1997, Foscarini and Brooks 1997, Klemens 2000, Moll and Moll 2004). Therefore, it is vital to not only conduct long-term population studies, but also to understand the life history characteristics of the species of interest in order to predict how populations or species are likely to respond to disturbances and various management actions (Frazer et al. 1991, 1993, Gibbons 1997, Heppell 1998, Hellgren et al. 2000). Despite the importance of such data, few long-term studies have been conducted or address these issues (Meylan et al. 1992, Congdon et al. 1993, Congdon et al. 1994, Foscarini and Brooks 1997, Dreslik 1998). The studies that have been conducted have primarily focused on a single chelonian species rather than on the entire turtle assemblage and studies of turtle communities remain relatively rare (Moll 1990, Moll and Moll 2004). Without the resultant population and life history characteristics data, conservation and management will continue to be sparse and inadequate and many species may become imperiled or more threatened (Trauth et al. 1998, Moll and Moll 2004).

The paucity of turtle community studies may, in part, be an artifact of turtle community species composition (Bury 1979, Moll and Moll 2004). In a review, Moll and Moll (2004) found that turtle communities were often skewed toward one or two numerous species and a smattering of rare species. Lotic habitats, for example, are often dominated by map turtles (*Graptemys* spp.) (Bury 1979, Moll and Moll 2004).

The Northern Map Turtle, *Graptemys geographica* (Le Sueur)

The northern map turtle, *Graptemys geographica*, is a relatively widespread, largely unstudied, diurnal species (Daigle et al. 1994, Ernst et al. 1994, Fuselier and Edds 1994, Moll and Moll 2004). *Graptemys geographica* occur from southern Quebec, Canada and northwestern Vermont, west of the Appalachian Mountains to southeastern Minnesota and eastern Kansas, to southern Arkansas and northern Alabama (Ernst et al. 1994; Figure 1-1). Isolated populations exist in Maryland, eastern New York, and eastern and central Pennsylvania (Ernst et al. 1994; Figure 1-1). Many accounts of this species are solely distributional (Arndt and Potter 1973, Kiviat and Buso 1977, Congdon and Gibbons 1996, Casper 1997, King et al. 1997, Walley 2000) and few historical population estimates are available to reassess population status (Roche 2002; but see Pitt 2005).

Considerable information gaps exist in the life history of this sexually dimorphic species (Gordon and MacCulloch 1980, Fuselier and Edds 1994, Roche 2002, Pitt 2005) and much of what is known of *G. geographica* is based on data from studies conducted in Ontario, Wisconsin, Pennsylvania, and Indiana (i.e., northern portions of the species' distribution) (Gordon and MacCulloch 1980, Vogt 1980a, 1981a, Iverson 1988, Nagle et al. 2004).

Graptemys geographica is a sexually dimorphic species in which females achieve much larger body proportions than males (Gordon and MacCulloch 1980, Lindeman and Sharkey 2001). Females are believed to reach sexual maturity at approximately 10 to 13 years of age,

while males mature in approximately four years (Vogt 1980a, Iverson 1988). The minimum plastron lengths of sexually mature females and males are estimated to be 17.5 cm and 7.5 cm, respectively (Gordon and MacCulloch 1980), though variation in minimum size of sexually mature *G. geographica* may occur throughout its distribution (Gordon and MacCulloch 1980, Iverson 1988). It has been estimated that *G. geographica* live for at least 20 years in the wild (Ernst et al. 1994).

Graptemys geographica occur in lakes, rivers, and streams with mud, rock, or gravel substrata, abundant vegetation, and ample sunlit basking sites of rocks and fallen trees (Gordon and MacCulloch 1980, Ernst et al. 1994, Fuselier and Edds 1994, Roche 2002). Within a habitat, *G. geographica* distribution may be associated with physiological constraints, predation risk, intra- and interspecific competition, social interactions, prey availability and distribution, and habitat structure (Boyer 1965, Vogt 1979, 1981a, Flaherty and Bider 1984, Pluto and Bellis 1986, Graham and Graham 1992, Daigle et al. 1994, Ernst et al. 1994, Saumure and Livingston 1994, Fuselier and Edds 1994, Vogt and Benitez 1997, Roche 2002). For example, Pluto and Bellis (1986) observed differential habitat utilization within a river between size classes of *G. geographica*. Large turtles (i.e., females) occupied deep, slow-moving sections with emergent rocks and logs (Pluto and Bellis 1986). Small turtles, which include both sexes, occupied shallow, slow-moving sections with ample emergent vegetation (Pluto and Bellis 1986). In this case, habitat partitioning reflected the maximum swimming speed associated with body size (Pluto and Bellis 1986). Larger turtles have a higher maximum swimming speed than smaller turtles and are able to navigate and rapidly move through the deeper water (Pluto and Bellis 1986). Correspondingly, habitat selection may have also reflected the relative predation risks associated with body size (Pluto and Bellis 1986). Juvenile *G. geographica* may use shallower

areas to avoid large predaceous fish and are able to avoid terrestrial predators by concealing themselves between rocks and small logs (Pluto and Bellis 1986) or among emergent vegetation (personal observation). Large turtles are relatively immune to aquatic predation during their active season and may avoid terrestrial predators, such as raccoons, by remaining in deep water, far from shore (Pluto and Bellis 1986).

Habitat partitioning may also be a mechanism for reducing competition between size classes for basking sites (Pluto and Bellis 1986), and social factors may be more important than habitat structure for basking site selection (Flaherty and Bider 1984). Basking is important to *G. geographica* for thermoregulation and parasite removal (Boyer 1965, Vogt 1979, Saumure and Livingston 1994) and may facilitate interspecific mutualisms (Vogt 1979). *Graptemys geographica* often cluster around basking sites and bask communally (Flaherty and Bider 1984). Communal basking may aid in predator avoidance as *G. geographica* are extremely wary baskers and readily retreat into water if even one of the group is disturbed (Daigle et al. 1994, Ernst et al. 1994, Roche 2002). In situations where basking habitat is limited, large turtles will displace smaller turtles (Pluto and Bellis 1986). Habitat is eventually partitioned by small turtles basking close to the shore and medium and large turtles basking midstream (Pluto and Bellis 1986). Medium and large turtles further partition basking sites by basking on smaller branches and the main trunk of trees, respectively, when space is limited (Pluto and Bellis 1986).

Ultimately, for *G. geographica* to even occur in an area, basic habitat requirements must be met. In addition to containing areas for basking, the aquatic habitat must also have a deep pool for *G. geographica* to congregate in hibernacula where courtship and mating occur in spring and fall (Pluto and Bellis 1988, Graham and Graham 1992, Roche 2002). These pools must

remain unfrozen and be deep enough to avoid ice scouring as *G. geographica* are mobile on the bottom of the hibernacula (Graham and Graham 1992).

Males leave the hibernacula in late spring and early summer in search of food (Pluto and Bellis 1988). Therefore, the aquatic system must provide ample prey to support them as well as the rest of the *G. geographica* population. Stomach content analysis and feeding observations have revealed a strictly aquatic diet of mollusks, insects, crayfish, fish carrion, and trace amounts of vegetation, which was probably consumed incidentally with prey and therefore not considered a food source (Vogt 1980a, 1981a, Ernst et al. 1994, Lindeman and Sharkey 2001, Moll 1976, Roche 2002). *Graptemys geographica*'s diet varies with prey availability, although this species is not abundant in areas with low mollusk densities (Vogt 1981a). Adult females' broad heads and jaws are physically adapted for a specialized mollusk diet (Vogt 1981a, Lindeman and Sharkey 2001), while adult males and juveniles are generally insectivorous (Vogt 1980a, 1981a, Lindeman and Sharkey 2001). In areas of high mollusk abundance, both genders and all size classes are primarily molluskivorous (Vogt 1981a, White and Moll 1992). In less prey-abundant locales, it appears that habitat and diet partitioning among genders and size classes and increased dispersal of males may be mechanisms employed to avoid competition (Pluto and Bellis 1986, 1988, Roche 2002). It has been hypothesized that distribution of *G. geographica* may be more limited by prey availability than habitat structure due to diet specialization (Vogt 1981a, Fuselier and Edds 1994, Vogt and Benitez 1997).

Gravid females tend to move upstream from hibernacula toward nesting sites (Gordon and MacCulloch 1980, Pluto and Bellis 1988), which may be a mechanism to offset the general downstream dispersal of hatchlings that occurs with the river's current (Pluto and Bellis 1988). Therefore, the aquatic habitat must be located proximate to terrestrial areas that contain ample

suitable nesting sites. Suitable nesting sites are generally located above the floodplain and are composed of soft sand or soil with good drainage and sun exposure, though sites with less desirable substrates have been used (Flaherty and Bider 1984, Roche 2002). Sun exposure and surrounding vegetation are important elements of nesting sites as *G. geographica* have temperature-dependent sex determination, with mean incubation temperatures of 25°C and 30.5°C producing males and females, respectively (Gordon and MacCulloch 1980). Additionally, low temperature nest sites may be associated with fly larvae (*Metoposarcophaga importuna*) infestation (Vogt 1981b). If suitable nesting habitat is in abundance, nesting site selection may be dictated more by social factors than physical attributes of a given area (Flaherty and Bider 1984).

Graptemys geographica populations are primarily threatened by pollution, habitat alteration and degradation, and exploitation (Ernst et al. 1994, Buhlmann and Gibbons 1997, Roche 2002). Pollution and alterations to the aquatic environment can cause a reduction of prey and basking site abundance (Gibbons 1997, Lindeman 1998, Moll and Moll 2004). Mollusks, the preferred prey of *G. geographica*, are extremely pollution-sensitive and can be suffocated by increased siltation associated with upland farming, urban runoff, and development (Ellis 1936, Dodd 1978, Ernst et al. 1994, Burkhead et al. 1997, Moll and Moll 2004). Chemical pollutants that do not eradicate prey may threaten *G. geographica* due to prey contamination and subsequent bioaccumulation (Kannan et al. 2000, Roche 2002). Prey abundance may also be compromised by hydrological changes created by impoundments or channelization (Moll and Moll 2004).

Graptemys geographica overall health and reproductive health in particular may be compromised by snag removal that is often associated with river ‘clean-up’ activities as fewer

basking sites will be available to facilitate thermoregulation (Buhlmann and Gibbons 1997, Roche 2002). Increased recreational use of an area may also effectively alter habitat by deterring use of structurally suitable basking sites (Gordon and MacCulloch 1980, Roche 2002).

Nesting sites can be destroyed by alterations to both the aquatic and terrestrial habitats. Impoundments may submerge upstream nesting areas (Roche 2002) forcing females to nest in suboptimal habitats. Suboptimal habitats include those with low sun exposure, an abundance of vegetation, highly compacted soil, improper water drainage, or location within a floodplain (Flaherty and Bider 1984, Roche 2002). Low incubation temperatures associated with inadequate sun exposure and abundant vegetation may result in skewed sex ratios (Vogt and Bull 1984). Improper water drainage and occasional flooding can drown or cause fly larvae infestation of eggs (Vogt 1981b), decreasing nest survival and subsequent recruitment. Terrestrial development may directly or indirectly destroy nesting sites (Roche 2002). Increased edge associated with development can increase populations of predators such as foxes, coyotes, raccoons, skunks, and opossums (Cochran 1987). Roads that must be crossed to reach nesting sites increase mortality of gravid females (Casper 1997, Roche 2002).

Exploitation is increasingly threatening *G. geographica* populations (Roche 2002). Historically, *G. geographica* meat was used to dilute terrapin meat (Arndt and Potter 1973). Currently, *G. geographica* are harvested for subsistence use (Moll and Moll 2004) and they are traded domestically to biological supply companies and internationally to pet and food markets (Moll and Moll 2004). From 1989 to 1993, total reported exports of *Graptemys* species increased from 73 to 37,233 individuals per year (Roche 2002). From 1998 to 2002, total reported exports of wild-caught *Graptemys* species consisted of 95,069 individuals (Schlaepfer et

al. 2005). Though these data are not specific to *G. geographica*, prevalence of *G. geographica* in the pet trade has been documented (Buhlmann and Gibbons 1997, Moll and Moll 2004).

In 2006, *G. geographica* was listed as an Appendix III species in Convention on International Trade in Endangered Species of wild fauna and flora (CITES) (U.S. Fish and Wildlife Service (USFWS) 2006), which includes “species that are protected in at least one country, which has asked other CITES Parties for assistance in controlling the trade” (CITES 2005). *Gratemys geographica* are currently protected throughout part of their range by state and provincial law (Buhlmann and Gibbons 1997, Roche 2002), but has never been evaluated for International Union for the Conservation of Nature and Natural Resources (IUCN) listing (Moll and Moll 2004).

***Gratemys geographica* in Missouri**

Gratemys geographica are protected by state law throughout Missouri (Moll and Moll 2004), a state in which it is widely distributed (Johnson 2000). *Gratemys geographica*'s range throughout Missouri includes all but the northern and southeastern portions of the state (Johnson 2000; Figure 1-2). Habitats include rivers, sloughs, and oxbow lakes with gravel bottoms, some aquatic vegetation, and ample basking sites (Johnson 2000). *Gratemys geographica* are typically active from late March to October, but has been observed basking in December and February (Johnson 2000). Mating is limited to spring months, with nesting occurring from late April to early July and hatching occurring in late summer, early autumn, or the following spring (White and Moll 1991, Johnson 2000).

Gratemys geographica's reproductive potential and diet have been studied in the Niangua River, Missouri (White and Moll 1991, 1992). In Missouri, *G. geographica* oviposits two to three clutches yielding a mean of 23.3 eggs per female per year (White and Moll 1991). *Elimia potosiensis*, a small gastropod, was the most abundant prey species consumed by both sexes and

all life stages of *G. geographica*, comprising 94.1% –100% of their diet by volume, the remainder consisting of crayfish and insects (White and Moll 1992). This specialized diet resulted in failure to catch *G. geographica* with fish-baited traps at the Niangua River site and may indicate a distribution limited by the availability of gastropods (White and Moll 1991).

Threats to *G. geographica* in Missouri are similar to those in other parts of their range. In addition, the Missouri Department of Conservation (MDC) found that shooting basking turtles for target practice was so common that they have posted signs and web pages discouraging this behavior (Moll and Moll 2004).

A population of *G. geographica* in the North Fork of White River (NFWR), Ozark County, Missouri, has been studied since 1969 (Pitt 2005), which represents the only long-term study of a northern map turtle population throughout their broad range. Pitt (2005) determined that the population had declined since 1969 and remained at this reduced size through 2004. The reduction in population size was attributed to a harvesting event or events that occurred between 1969 and 1980 (Pitt 2005). The inability of the population to rebound was reflective of factors associated with the initial loss of the large, and therefore the most fecund, females; habitat and water quality degradation; reduction of basking habitats; increased recreational use of the river; and the establishment of red-eared sliders (*Trachemys scripta elegans* Wied-Neuwied) (Pitt 2005). In association with the *G. geographica* population decline and changes in aquatic habitat, the chelonian community composition changed, supporting a larger relative proportion of generalist species (Pitt 2005).

North Fork of White River, Ozark County, Missouri

The North Fork of White River is a 99.8 km long river with a 1478.9 km² watershed (Bryant Watershed Project, Inc. 2008). The majority of the watershed is characterized by grassland/cropland and forest/woodland with about 13% consisting of Mark Twain National

Forest lands (Bryant Watershed Project, Inc. 2008). The North Fork of White River receives a large volume of water from several major springs, which creates a substantial temperature gradient along the river's length (Nickerson and Mays 1973).

In general, rivers are spatially and temporally dynamic (Pluto and Bellis 1988, Moll and Moll 2004). A spring-fed river, such as NFWR, is particularly spatially variable because of the thermal gradients produced by the spring effluents. Due to the sometimes specialized habitat requirements of turtles (Ernst et al. 1994), it may be expected that turtle communities and populations differ within various sections of the same river. The turtle community within the North Fork of White River, Ozark County, Missouri, has been studied periodically since 1969 (Pitt 2005). Studies have largely been confined to a 4.6 km section of NFWR (Pitt 2005) and few data are available outside of that area. No thorough investigations of turtle communities in different sections of the river have been conducted.

Due to the unique thermal characteristics of NFWR, it is possible to evaluate how natural thermal regimes affect turtle populations. Temperature has been implicated as a cause of variation in digestion, ingestion, and assimilation rates, which may lead to differences in growth rate among individuals and populations (Ellis 1936, Cagle 1946, Gatten 1974, Ernst 1975, Parmenter 1980, Thornhill 1982, Spotila et al. 1984, Brown and Brooks 1991, Frazer et al. 1993, Brown et al. 1994, Cadi and Joly 2003). Increased growth rates can lead to larger body sizes at various life stages and earlier maturation. Both factors may influence fitness via survival and reproductive enhancements (Bury 1979, Thornhill 1982, Congdon and Gibbons 1983, 1990, Cox et al. 1991, Congdon and Gibbons 1996, Lovich et al. 1998, Tucker et al. 1999, Tucker 2000). By identifying variations in growth rate, it is possible to identify where variation in other life history traits can occur (Frazer et al. 1991, 1993). To date, studies of variation in population

growth rates within a river affected by a naturally-induced thermal gradient are not available in peer-reviewed literature. NFWR presents a unique opportunity to assess temporal and spatial variation in growth rate and associated parameters in naturally thermally-distinct areas.

Objectives

- **Determine whether turtle communities and populations located within a river with a natural thermal gradient vary temporally and spatially.**

Rationale: Theory has shifted focus from classic ideas of stable and relatively static communities and populations to concepts describing temporally and spatially dynamic entities (Chesson and Case 1986, Pimm 1991). NFWR provides a unique opportunity to explore spatial and temporal variability in river turtle communities and populations. To date, few studies explore spatial and temporal variation of river turtle communities and populations (but see Moll 1977, Shively and Jackson 1985, Moll 1990, Huestis and Meylan 2004, Pitt 2005). Even fewer studies present data dating back several decades (but see Moll 1977, Huestis and Meylan 2004, Pitt 2005).

In Chapter 2, I used the rarefaction method to examine species richness in each community. I evaluated heterogeneity of the communities, which encompasses both species richness and evenness, using Simpson's index modified for a finite population. Population analyses were restricted to *G. geographica*, the numerically-dominant species in each community. I calculated Schumacher-Eschmeyer population estimates for *G. geographica* and compared the population estimates using the Chapman and Overton method.

- **Determine whether species distribution is associated with particular microhabitats.**

Rationale: Community composition is determined by abiotic and biotic factors which can be difficult to measure in natural settings (Diamond 1986, Roughgarden and Diamond 1986). *In situ* turtle studies in particular often rely on traps for collection (see Lagler 1943, Plummer 1979,

Vogt 1980b for trap descriptions) which do not allow for behavioral or microhabitat observations. In this study, capture methodology allowed for direct observation of turtle behavior and microhabitat use prior to disturbance by surveyors. Capture techniques allowed for behavior and microhabitat elements to be categorized.

I compared broad-scale river characteristics to elucidate factors that differed among the turtle community and populations' habitats. For each species, I summarized the activity, water depth, and associated microhabitat structures. For species observed basking, I calculated Levins' standardized niche breadth measure and Pianka's niche overlap index based on basking substrate. These data are presented in Chapter 2.

- **Determine whether instantaneous growth rates of *Graptemys geographica* vary temporally and spatially in a river with a natural thermal gradient.**

Rationale: Phenotypic plasticity in traits that can directly influence life history parameters is important for organisms that live in variable ecosystems (Caswell 1983, Stearns and Koella 1986). Growth rate is a trait that can vary with the thermal environment of ectotherms, such as turtles (Laudien 1973, Lillywhite et al. 1973, Gibbons et al. 1981, Bronikowski et al. 2001). Plasticity in growth rate may have important implications for turtles as global climate change is resulting in overall warming trends (Schlesinger and Jiang 1991, Manabe and Stouffer 1993, Intergovernmental Panel on Climate Change 2007). Variations in growth rate can lead to size-related alterations in survival and fecundity that can last throughout a turtle's life (Gibbons et al. 1981, Stearns and Koella 1986).

Differences in growth rate have been observed in turtle species subjected to thermal effluents associated with power plants (Parmenter 1980, Gibbons et al. 1981, Thornhill 1982). No investigations of turtle growth rates in a river with a natural thermal gradient have been published. Temporal variation in growth rate has been identified for northern turtle populations

and attributed to global climate change (Frazer et al. 1991, 1993). No investigations of turtle growth rates have been reported for populations in the central United States.

NFWR provided a unique opportunity to examine whether temporal and spatial differences in growth rates of river turtles occur. In Chapter 3, I compared instantaneous growth rates and body temperature of *G. geographica* inhabiting two thermally distinct sections of NFWR. I also examined differences in instantaneous growth rates for temporally distinct *G. geographica* populations. I investigated whether observed growth rate trends corresponded with climate trends.

- **Determine the age at maturity of *G. geographica* using a statistical method.**

Rationale: Statistically-generated growth curves based on field observations provide estimates of age at sexual maturity and highlight differences in life history characteristics between sexes and among populations and taxa (Frazer et al. 1990a, Lindeman 1997).

In Chapter 4, I used data from previous and current studies of *G. geographica* in NFWR to evaluate whether the temporal differences in instantaneous growth rates observed translated into differing growth curves. I used the results to discuss general observed trends and potential implications of global warming on turtle growth.

In Chapter 5, I integrated information presented in previous chapters to draw conclusions and recommendations applicable to future turtle studies both within and outside of NFWR.

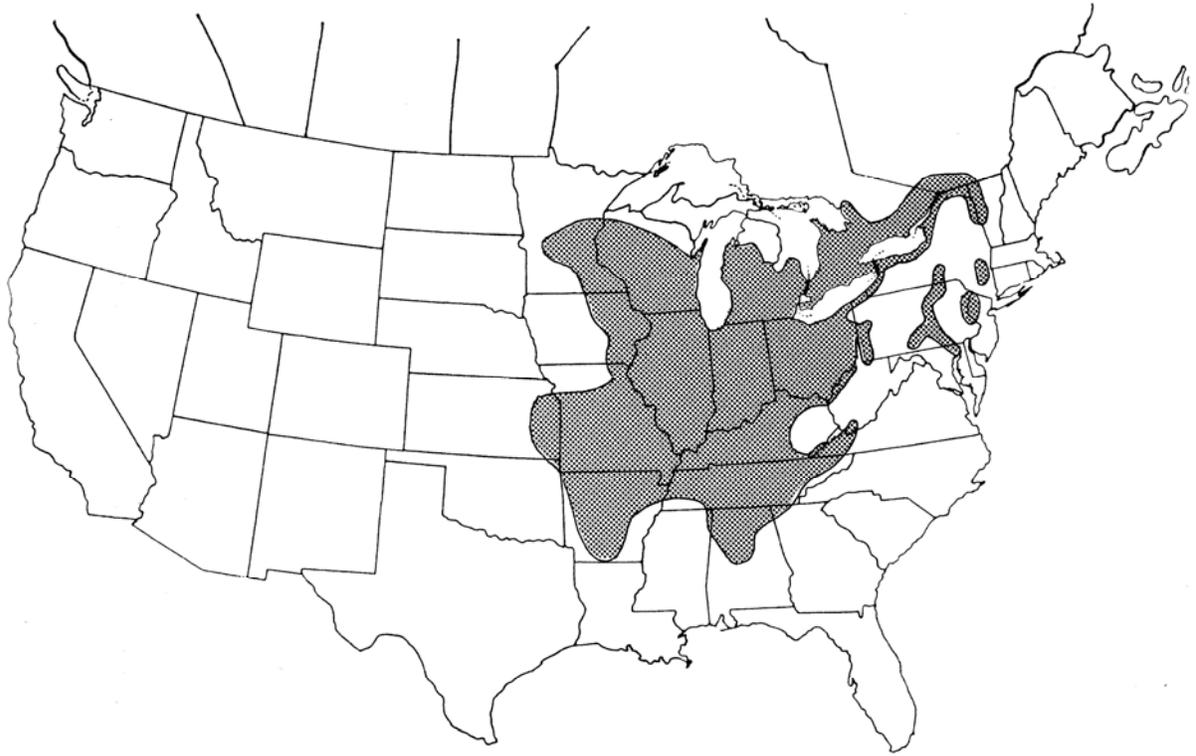


Figure 1-1. Distribution of the northern map turtle, *Graptemys geographica*, in North America
Range map for *Graptemys geographica* reproduced from Ernst, C. H., J. E. Lovich,
and R. W. Barbour. 1994. *Turtles of the United States and Canada*. Smithsonian
Institution Press, Washington D.C. and London. Pp. 369. Used with permission of
the author.

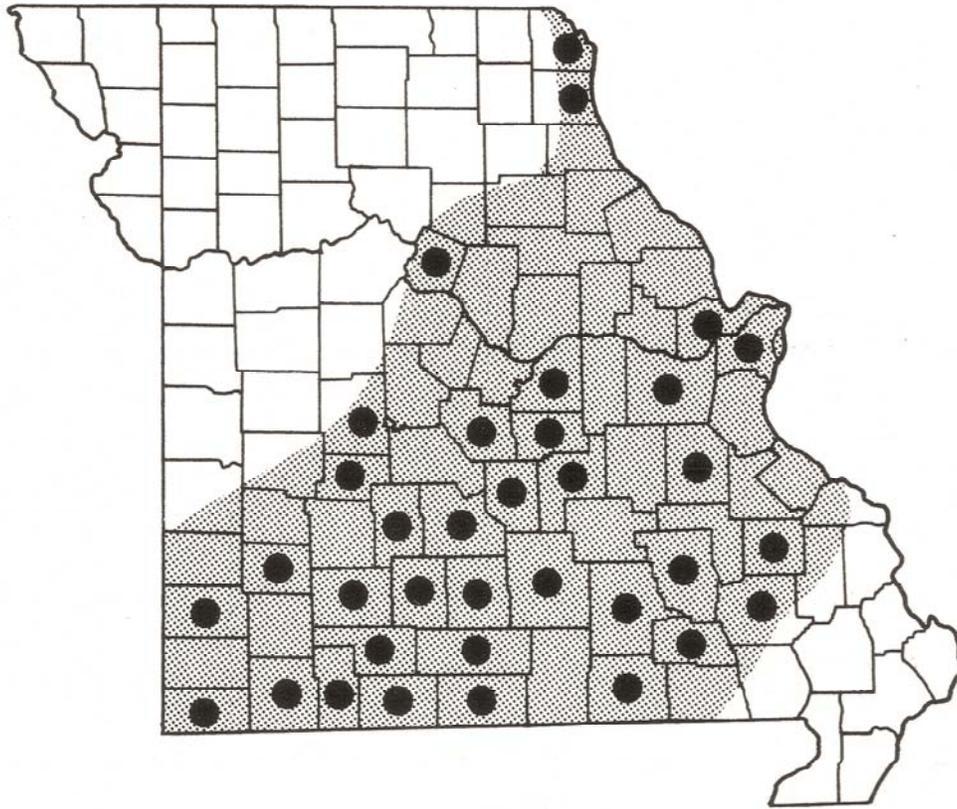


Figure 1-2. Distribution of the northern map turtle, *Graptemys geographica*, in Missouri (Johnson 2000). Shading indicates the suspected range of *G. geographica*. Black dots signify areas for which county records exist. Range map for *Graptemys geographica* reproduced from "The Amphibians and Reptiles of Missouri." Pp. 194. Copyright 2000 by the Conservation Commission of the State of Missouri. Used with permission.

CHAPTER 2
FRESHWATER TURTLE POPULATIONS AND COMMUNITY COMPOSITION IN TWO
THERMALLY DISTINCT SECTIONS OF A RIVER

Introduction

Theory has shifted focus from classic ideas of stable and relatively static communities and populations (i.e. equilibrium theories) to concepts describing temporally and spatially dynamic entities (i.e., nonequilibrium theories) (Chesson and Case 1986, Pimm 1991). This shift can largely be attributed to the idea that the environment (i.e., abiotic factors) is perpetually changing (Chesson and Case 1986). Changes in abiotic conditions can alter biotic conditions as organisms' physiological tolerance thresholds are met and species composition turnover occurs (Davis 1986, Cody 1996). The resultant fluctuations in identity and relative abundance of species can alter community dynamics and composition (Cody 1996).

Abiotic and biotic factors can vary in space and time (Wiens 1984, Wiens et al. 1986, Pimm 1991, Cody 1996). Variation can occur over large or small scales (Wiens 1984, Wiens et al. 1986, Cody 1996). Variation can be associated with natural processes, such as those related to hydrology, geology, climate, competition, predation, or disease (Wiens 1984, Cody 1996), but can also be a result of what are typically deemed unnatural processes associated with human activity (Cody 1996).

Rivers are the epitome of spatially and temporally dynamic systems (Moll and Moll 2004, Pluto and Bellis 1988). Geologic composition can differ along a river's length (Schumm 2005). Hydrological regimes can swiftly change (Schumm 2005). Rivers can span great distances (Schumm 2005) and flow through different climatic zones. Most rivers have undergone massive alterations by humans (Benke 1990, Ricciardi and Rasmussen 1999). Damming, riparian zone alterations, and pollution only scratch the surface of human-based river modifications (Lydeard and Mayden 1995, Ricciardi and Rasmussen 1999). Due to the inherent variability of rivers,

populations and communities can change considerably along the length of a river and within a small area of a river throughout time (Kinsolving and Bain 1993, Moll and Moll 2004).

The North Fork of White River (NFWR), Ozark County, Missouri is a 99.8 km long river with a 1478.9 km² watershed (Bryant Watershed Project, Inc. 2008). The majority of the watershed is characterized by grassland/cropland and forest/woodland (Bryant Watershed Project, Inc. 2008). Approximately 13% of the watershed consists of Mark Twain National Forest lands (Bryant Watershed Project, Inc. 2008). NFWR receives a large volume of water from several major springs (Nickerson and Mays 1973). The springs' effluents create a temperature gradient along the stream's length (Nickerson and Mays 1973).

Within Ozark County, the land bordering the section of NFWR upstream of the major springs is largely national forest land and remains predominantly forested (Bryant Watershed Project, Inc. 2008). The land bordering the section of NFWR downstream of the major springs has been progressively developed for resorts and private residences (Pitt 2005, personal observation).

The turtle community within a 4.6 km section of NFWR located downstream of the major springs has been studied periodically since 1969 (Pitt 2005). These studies indicate that NFWR supports a diverse turtle community predominated by the northern map turtle, *Graptemys geographica* (Le Sueur) (Pitt 2005). A decline in the *G. geographica* population occurred between 1969 and 1980 (Pitt 2005). A comparison of population estimates indicated the *G. geographica* population observed in 2004 had not rebounded from the reduced 1980 population size (Pitt 2005). Between 1969 and 1980, a new species, the red-eared slider (*Trachemys scripta elegans* Wied-Neuwied) joined the community within the research section (Pitt 2005). Changes in community composition were attributed mainly to harvesting of *G. geographica* (Pitt 2005).

Confounding factors included otter reintroductions, fibrous algae blooms, a reduction in basking habitats, an increase in recreational use of the river, changes in the distribution of stream substrates, siltation, sedimentation, nutrient-loading, fecal coliform contamination, pesticide inputs, and loss of large boulders (Pitt 2005).

River turtle populations and communities, like all organisms, are influenced by a suite of abiotic and biotic factors (Moll 1990, Ernst et al. 1994, Bodie and Semlitsch 2000, Bodie et al. 2000, Moll and Moll 2004). Abiotic factors include hydric regimes, thermal regimes, permanence, habitat complexity, substrate composition, chemistry of the water body, and land use of the adjacent land (Moll 1990, Bodie et al. 2000, Moll and Moll 2004). Biotic factors encompass each species' phylogeny, physical adaptations and capabilities, life history characteristics, and habitat preferences, as well as inter- and intraspecific competition, predation, and resource (e.g., prey) availability (Moll 1990, Bodie et al. 2000, Moll and Moll 2004). Because turtle species can have specialized habitat requirements (Ernst et al. 1994) and because rivers can vary greatly along their length (Schumm 2005), I predict that turtle communities differ among various sections of the same river. Spring-fed rivers, such as NFWR, are particularly spatially variable because of the thermal gradients produced by the spring effluents. Therefore, I predict that differences in turtle communities can occur over short distances.

NFWR provides a unique opportunity to explore spatial and temporal variability in river turtle communities and populations. This type of data is increasingly important as turtle populations are declining worldwide (Smith 1979, Moll 1986, Kuchling 1988, Ernst et al. 1994, Buhlmann and Gibbons 1997, Gibbons 1997, Haitao 2000, van Dijk et al. 2000, Moll and Moll 2004) and there is little information about the ecology, population status, and community composition of many turtle species and assemblages (Moll 1990, Ernst et al. 1994, Moll and

Moll 2004). To date, few studies explore spatial and temporal variation of river turtle communities and populations (but see Moll 1977, Shively and Jackson 1985, Moll 1990, Huestis and Meylan 2004, Pitt 2005). Even fewer studies present data dating back several decades (but see Moll 1977, Huestis and Meylan 2004, Pitt 2005). Without these data, it may be impossible to garner political, social, and financial support for conservation of imperiled chelonians (Gibbons 1997).

It was my objective to: 1. Determine whether turtle communities and populations located within a river with a natural thermal gradient vary in time and space and, 2. Determine if species distribution is associated with particular microhabitats or abiotic factors.

Materials and Methods

I selected two research sections within the NFWR based on their physical similarities, ease of access, and locations relative to the major spring-flows. The first area is the 4.6 km section studied by Nickerson and Mays (1973) and Pitt (2005). This section is located downstream of the major springs and is relatively cool for much of the year, especially during the summer months. A relatively large amount of historical data exists for this section. The second area is a 4.6 km section located upstream of the springs and is relatively warm. The upstream area is located within Mark Twain National Forest. The only development adjacent to the upstream study section is the boat ramp and campground operated by the National Forest ranger district. This clearing is located at the upstream end of the upstream research section. The two research sections are separated by approximately 16 river kilometers.

I divided each of the two 4.6 km study sections into fifty 92-m-long stations, following the protocol of Nickerson and Mays (1973). In 2005, I recorded stream width, water depth, substrate composition, and the presence or absence of aquatic vegetation for each of the two research sections. I measured stream widths as the distance between banks at each station marker along

each of the 4.6 km research sections. I recorded water depth, substrate composition, and vegetation for midstream and one meter from each bank at each station marker. I compared stream widths and depths using independent sample t-tests to determine if mean values were significantly different between the two sites. I summarized and compared substrate composition and vegetation presence using chi-squared tests of homogeneity. In 2007, I collected water samples within each research section and the local springs. I analyzed water samples for total coliform bacteria and *Escherichia coli* content using the Coliplate™ test (Bluewater Bioscience, Inc. Mississauga, ON, Canada).

In 2005, 2006, and 2007, a research assistant and I surveyed the research sections on alternating days throughout the summer (June 15 to August 20) between 0900 and 1800 h, weather permitting. The downstream section was surveyed for a total of 415 person hours. The upstream section was surveyed for a total of 351 person hours. I recorded water temperatures at the beginning of each sampling day. I used an independent sample t-test to determine whether water temperatures were significantly different.

Surveys were conducted primarily by snorkeling paired with mark-recapture techniques. Snorkeling is useful for capturing basking turtles, such as *G. geographica*, that are otherwise difficult to trap. Methods that rely on traps (see Lagler 1943, Chaney and Smith 1950, Braid 1974, Vogt 1980b) are less effective for basking turtles (Cagle 1942, Frazer et al. 1990b), especially *G. geographica*, which may not respond to bait (Lagler 1943) and are wary of traps (Pluto and Bellis 1986). Additionally, traps (see Lagler 1943, Chaney and Smith 1950, Vogt 1980b) are time consuming to assemble, cumbersome, and difficult to use in a heavily-trafficked stream like the North Fork (Pluto and Bellis 1986). Trapping also does not allow for direct observations of behavior. Despite the difficulties and shortcomings associated with traps, I set

two 0.75 m and two 1.0 m diameter hoop nets in areas in which many turtles were routinely observed once a week between 1800 and 0900 h in 2005 and 2006. Traps were set in each research section for several weeks to capture non-basking and nocturnal species. Traps were not set during the day or during the weekends due to the heavy recreational use of the stream (Pitt 2005). I baited traps with sardines. I discontinued the use of traps as they were ineffective.

All captured turtles were weighed, measured, and marked using nail polish, following the protocol of Pitt (2005). Larger turtles (plastron length ≥ 8.6 cm) were also marked with a passive integrated transponder (PIT) tag (Destron-Fearing Corporation, So. St. Paul, MN, USA) injected into the anterior inguinal region parallel to the bridge of the shell following the protocol of Buhlmann and Tuberville (1998). I disinfected injection sites and needles using 70% isopropyl alcohol and antibiotic ointment. I applied New-Skin Liquid Bandage (Medtech Laboratories, Inc., Jackson, WY, USA) to cover the injection hole. Previous studies from the downstream section of NFWR indicated that both paint marks and PIT tag retention were high (Pitt 2005) and therefore appropriate for the purposes of this study. I determined turtles' sex visually when possible based on morphology. Diagnostic characteristics used included tail length and thickness, relative position of the anal opening, and foreclaw characteristics. I categorized behavior as either basking or submerged. If turtles were basking prior to capture, I recorded the basking substrate. I categorized basking substrates as branch, log, live tree, rock, vegetation, freely-floating vegetative debris (e.g., leaves, small twigs), or riverbank. I recorded water depth at each capture location. I noted location of turtles within the research section in order to detect movement patterns.

I measured species richness of each turtle community sampled in NFWR using the rarefaction method. The rarefaction method allows comparison of communities from which

unequal sample sizes were collected (Krebs 1989). I used Program RAREFACT Version 1.0 (Krebs 1989) to complete the calculations for the rarefaction method. No spiny softshell turtles, *Apalone spinifera* (Le Sueur), were captured from the upstream section of NFWR in 2007. However, I observed at least five *A. spinifera* regularly within the upstream section in 2007. Therefore, I calculated an additional rarefaction curve for the turtle community present in the upstream section of NFWR in 2007 corrected for the failure to capture any of the regularly observed *A. spinifera* (i.e., I added five *A. spinifera* to the turtle community composition of the upstream section captured in 2007).

I assessed heterogeneity, which accounts for species richness and evenness (Krebs 1989), by using Simpson's Index of Diversity modified for a finite population and the reciprocal of Simpson's Index of Diversity. Simpson's Index of Diversity, also known as Hurlbert's Probability of Interspecific Encounter (PIE) (Hurlbert 1971) is the complement of Simpson's original index (Krebs 1989). Simpson's Index of Diversity is the most meaningful species diversity index as it equals the slope of the rarefaction curve at its base (Olezewski 2004). The reciprocal of Simpson's Index of Diversity was also calculated as it is easily interpreted as the number of equally common species required to obtain the calculated value of heterogeneity (Krebs 1989). I used Program DIVERS Version 1.1 (Krebs 1989) to calculate Simpson's Index and the reciprocal of Simpson's Index.

I used Program NICHE Version 1.1 (Krebs 1989) to calculate niche breadth using Levins' standardized niche breadth measure and the number of frequently used basking substrates.

To run programs RAREFACT Version 1.0, DIVERS Version 1.1, and NICHE Version 1.1 (Fortran program codes available in Krebs 1989), I used the GNU Fortran compiler, gfortran (Free Software Foundation, Inc., Boston, MA, USA), to create a Microsoft Windows XP

(Microsoft Corporation, Redmond, WA, USA) executable program. I updated the program source codes for the compiler by changing the specifier (i.e., IN, IO) for standard input in READ statements and standard output in WRITE statements to "*" (asterisk). I further modified the DIVERS Version 1.1 (Krebs 1989) program code by removing lines 6 – 7 and 125 – 129. Lines 6 – 7 and 125 – 129 implemented a loop that allowed for entry of multiple data sets in one run of the program. The compiler had difficulty with the data types used on those lines and their removal did not affect the calculations performed by the program. I also modified the NICHE Version 1.1 (Krebs 1989) program code by changing the format of line continuations from using an "*" (asterisk) to using a single digit in column 6.

I summed basking substrate use by species for each sample year. To assess whether species were partitioning basking substrates, I calculated estimates of Pianka's Niche Overlap Index using EcoSim: Null models software for ecology version 7 (Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT, USA). I set model parameters as follows: niche breadth: retained; zero states: reshuffled; resource states: equiprobable; random number seed: 10; iterations: 1000.

I used one-way analyses of variance (ANOVA) to identify differences in water depth use among *G. geographica* partitioned by sex located in the downstream section in 1969 to 1972 and in the upstream section in 2005 to 2007. I used one-way ANOVA to compare differences in water depth use among *G. geographica*, stinkpots (*Sternotherus odoratus* Latreille), and *T. s. elegans* partitioned by sex in the downstream section in 2005 to 2007. I used Tukey's post-hoc procedure to determine significantly different samples. Analyses were limited to *G. geographica* in both sections in all years and *T. s. elegans* and *S. odoratus* located in the downstream section in 2005 to 2007 due to sample size.

Species-specific statistical analyses of turtle data were limited to *G. geographica* due to larger sample sizes. I calculated population size estimates with 95% confidence intervals for *G. geographica* using the Schumacher-Eschmeyer method (Krebs 1989). I compared the population estimates using the Chapman and Overton method (as described in Seber 1982) to identify significant differences (two-tailed test with 5% level of significance) between research sections. I calculated standardized density estimates using the Schumacher-Eschmeyer estimated population sizes and the areas calculated from the products of the mean stream widths and lengths of research sections. I conducted independent sample t-tests and analyses of variance (ANOVA) to determine whether the mean plastron length of the *G. geographica* populations, partitioned by sex, varied among sampling years when assumptions of normality and equal variance were met. I tested assumptions of normality and equal variance using the Kolmogorov-Smirnov and Levene analyses, respectively. I used nonparametric Mann-Whitney U and Kruskal-Wallis tests when assumptions of normality and equal variance were not met. I used binomial tests to identify if sex ratios of each population differed from 1:1 (male: female) in any sampling year. I used chi-squared (χ^2) tests of independence to identify if sex ratios differed between populations or among sampling years within each population. I used SPSS version 11.5 (SPSS Inc., Chicago, IL, USA) with $\alpha = 0.05$ to perform all statistical analyses.

Results

The downstream section was significantly wider than the upstream section (mean = 43.4 m and 28.4 m, respectively; $t = 7.438$, $df = 93$, $p = 0.000$). Midstream water depth was significantly deeper in the downstream than in the upstream section (mean = 76.41 cm and 60.92 cm, respectively; $t = 2.195$, $df = 96$, $p = 0.031$). A similar significant pattern was observed when comparing water depths taken one meter from the east bank ($mean_{downstream} = 38.69$ cm,

mean_{upstream} = 25.14 cm; $t = 3.369$, $df = 96$, $p = 0.001$). No significant difference was observed between values measured one meter from the west bank (mean_{downstream} = 35.06 cm, mean_{upstream} = 35.04 cm; $t = 0.005$, $df = 96$, $p = 0.996$).

The stream substrate characteristics in both research sections did not differ from the historical description of the downstream section offered by Nickerson and Mays (1973) with the exception of silt and sediment deposits (but see Pitt 2005 for differences in substrate distribution in the downstream section). Substantial silt and sediment deposits were not observed in previous studies (Nickerson and Mays 1973), but were apparent in both research sections in similar proportions ($\chi^2 = 0.2562$, $df = 1$, $p > 0.10$) in 2005. Floating algal masses, submerged fibrous algal growths, and emergent vegetation stands were also apparent in both study sections, though amounts were significantly higher in the downstream section ($\chi^2 = 0.7941$, $df = 1$, $p < 0.005$).

Total coliform levels exceeded the values deemed safe for full body contact by the Missouri Department of Natural Resources (MDNR) (2005; Figure 2-1) in 34 of the 46 individual water samples collected from the research sections and springs. Fourteen of the 46 water samples also surpassed safe levels of *E. coli* content for full body contact (MDNR 2005; Figure 2-2).

Water temperatures were significantly cooler in the downstream section than in the upstream section (mean = 18.7 °C and 23.7 °C, respectively; $t = -16.9$, $df = 74$, $p = 0.000$).

Graptemys geographica was the most abundant turtle species in both study sections in all years (Figures 2-3A and B). *Trachemys scripta elegans* and *S. odoratus*, composed a higher percentage of the turtle community in the downstream section than in the upstream section in 2005 – 2007 (Figures 2-3A and B). Their presence in the downstream section has steadily increased since previous studies (Pitt 2005). River cooters, *Pseudemys concinna* (Le Conte), and

snapping turtles, *Chelydra serpentina* (Linnaeus), were found in low numbers in both sections (Figures 2-3A and B). A small population of *A. spinifera*, was consistently observed basking in the upstream section during all sampling years, though sampling methods were not conducive to their capture and their presence is not accurately described by Figure 2-3B. Hand-capturing *A. spinifera* is difficult due to their fast swimming speed. Furthermore, the hoop traps failed to catch any turtles in either section and the bait was quickly consumed by non-target species, such as crayfish. Only one *A. spinifera*, a hatchling, was ever observed in the downstream section in recent years (Figure 2-3A). One alligator snapping turtle, *Macrochelys temminckii* (Harlan), was found in the upstream section in both 2006 and 2007 (Figure 2-3B). This species was never observed in the downstream section in prior studies.

Rarefaction curves representing the expected number of species observed in specified sample sizes drawn from the turtle communities in NFWR are presented in Figures 2-4A-H. The turtle community in the downstream section in 1969 had a higher than expected number of species for sample sizes greater than 40 individuals than that predicted for the communities in the same section in recent years (Figure 2-4A). As sample size increased, the expected number of species observed in the downstream section converged to approximately five species in all years except 2005 (Figure 2-4A). The rarefaction curve for the downstream community in 1969 leveled off at sample sizes greater than 60 individuals (Figure 2-4A and B). The rarefaction curves for the upstream community in recent years showed little tendency of leveling off with increasing sample size (Figure 2-4B). A higher expected number of species was predicted for all sample sizes for the upstream section than for the downstream section in 2005 (Figure 2-4C). A higher expected number of species was predicted for sample sizes greater than 50 individuals for the upstream section than for the downstream section in 2006 (Figure 2-4D). A lower expected

number of species was predicted for sample sizes less than 115 individuals for the upstream section than for the downstream section in 2007 (Figure 2-4E). However, if the turtle community in the upstream section was corrected for the failure to capture *A. spinifera*, the rarefaction curve was shifted upwards (Figure 2-4F). The corrected rarefaction curve resulted in a higher expected number of species in the upstream section than in the downstream section for sample sizes larger than 70 individuals (Figure 2-4F). Figures 2-4G and H illustrate how the rarefaction curve for the turtle community in the upstream section in 2007 shifted from being below to being almost identical to the curve for the community in the same section in 2006.

Comparison of Simpson's index revealed the turtle community in the downstream section is more diverse than the community in the upstream section (Table 2-1). The turtle communities in the downstream section in recent years were more diverse than the community observed in 1969 (Table 2-1).

All species except *M. temminckii* were observed basking at least once during the study period (Table 2-2). More than half of all *G. geographica* from any of the observed populations were basking prior to capture (Table 2-2). The downstream section in 2005 to 2007 was the only community in which species other than *G. geographica* were in high enough abundance to evaluate basking substrate use (Table 2-2). In the downstream community, 97.7 % of all *S. odoratus* captured in 2005 to 2007 were observed basking (Table 2-2). Of the *S. odoratus* observed basking, 96.9% were basking on vegetation (Table 2-2). The majority (76.5%) of *T. s. elegans* captured from the downstream community in 2005 to 2007 were observed basking (Table 2-2). Niche breadth analysis based on basking substrate use indicated that *G. geographica* had the widest niche breadth (Table 2-3). *Sternotherus odoratus* observed in recent

years had the narrowest niche breadth of species for which niche breadth was evaluated (Table 2-3).

Results of Pianka's niche overlap analyses are presented in Table 2-4. Pianka's niche overlap index assigns a value of 0.0 (no overlap) to 1.0 (complete overlap) to pairs of species. The only significant results obtained from the niche overlap analyses were from the downstream section in 2005 to 2007 (mean niche overlap = 0.789, probability observed mean overlap is due to chance = 0.000; variance of niche overlap = 0.02807, probability the observed variance in overlap is due to chance = 0.002) (Table 2-4).

Comparisons of water depth at capture site were limited by sample size for each species (Table 2-5). No significant difference in water depth use was observed among male, female, or indeterminate sex (i.e., indistinguishable sex based on external characteristics, hatchlings and post-hatchlings) *G. geographica* in the downstream section in 1969 to 1972 ($F = 1.889$, $p = 0.163$) (Table 2-6). *Graptemys geographica* for which sex was visually indistinguishable used significantly shallower water than males and females in the upstream section in 2005 to 2007 ($F = 25.244$, $p = 0.000$; Tukey's $p_{\text{indeterminate sex:females}} = 0.000$, $p_{\text{indeterminate sex:males}} = 0.000$, $p_{\text{females:males}} = 0.890$) (Table 2-6). Comparison of *G. geographica*, *S. odoratus*, and *T. s. elegans*, partitioned by sex, in the downstream section in 2005 to 2007 revealed that water depth use was significantly different ($F = 10.020$, $p = 0.000$) (Table 2-6). Tukey's post hoc analysis indicated that *G. geographica* for which sex was visibly indistinguishable used significantly shallower water depths than all other species and sexes, except *T. s. elegans* for which sex was visibly indistinguishable and *T. s. elegans* males (Table 2-7). *Trachemys scripta elegans* for which sex was visibly indistinguishable used significantly shallower water depths than male *G. geographica* and female *T. s. elegans* (Table 2-7).

The annual *G. geographica* population estimates in the downstream section (Table 2-8) were not significantly different (2005 and 2006: $z = 1.94$, $p > 0.025$; 2006 and 2007: $z = 0.89$, $p > 0.18$). The annual *G. geographica* populations estimates for the upstream section (Table 2-8) were significantly different (2005 and 2006: $z = 2.32$, $p < 0.02$; 2006 and 2007: $z = 2.14$, $p < 0.02$). The *G. geographica* population estimates between sections (Table 2-8) were not significantly different in any sampling year (2005: $z = 0.12$, $p > 0.45$; 2006: $z = 0.24$, $p > 0.40$; 2007: $z = 1.19$, $p > 0.11$). The validity of the population estimates is dependent on the nature of the data in correspondence with the assumptions of the model. Assumptions of the Schumacher-Eschmeyer method are: 1. the population is closed, 2. all animals have the same probability of getting captured, 3. marks do not affect catchability, 4. marks are not lost during sampling periods, and 5. all marked individuals are reported (Krebs 1989). The assumption that the population is closed is valid if movement into and out of the study area are equal and natality and mortality are equal. The assumption of a closed model was partially supported by the limited movement observed. Despite the prevalence of hatchlings in some years, it is likely that high hatchling mortality, typical of freshwater turtles, negates the potential recruitment effect. The assumption of equal catchability of marked and unmarked individuals appeared to be valid, except for adult females, which may have been more wary after the initial capture. Visibility of nail polish marks compensated for this increased wariness. The assumption that marks were not lost throughout the sampling period was confirmed by the retention of both painted marks and PIT tags by dually-marked individuals. All marked individuals were recorded, fulfilling the final assumption.

No significant differences were observed within or between the mean plastron lengths, separated by sex, of the downstream and upstream *G. geographica* populations in any year

(downstream males 2005 – 2007: $F = 1.118$, $p = 0.33$; downstream females 2005 – 2007: $\chi^2 = 2.379$, $df = 2$, $p = 0.30$; upstream males 2005 – 2007: $\chi^2 = 3.030$, $df = 2$, $p = 0.22$; upstream females 2005 – 2007: $\chi^2 = 2.428$, $df = 2$, $p = 0.30$; upstream and downstream males 2005: $t = -0.068$, $df = 36$, $p = 0.95$; upstream and downstream males 2006: $z = -0.128$, $p = 0.90$; upstream and downstream males 2007: $t = 1.337$, $df = 78$, $p = 0.19$; upstream and downstream females 2005: $z = -0.0877$, $p = 0.38$; upstream and downstream females 2006: $z = -0.818$, $p = 0.41$; upstream and downstream females 2007: $z = -1.160$, $p = 0.246$) (Figures 2-5A and B, Table 2-9).

Sex ratios of *G. geographica* for which sex was distinguishable did not differ significantly from 1:1 (male:female) in any population in any sampling year (Downstream: 2005: $p = 0.188$; 2006: $p = 0.237$; 2007: $p = 0.054$; Upstream: 2005: $p = 0.652$, 2006: $p = 1.000$, 2007: $p = 0.798$) (Figure 2-6). Sex ratios of *G. geographica* for which sex was distinguishable were not significantly different between sampling sites (2005: $\chi^2 = 2.25$, $df = 1$, $p > 0.05$; 2006: $\chi^2 = 1.14$, $df = 1$, $p > 0.05$; 2007: $\chi^2 = 1.16$, $df = 1$, $p > 0.05$) (Figure 2-6). Sex ratios of *G. geographica* for which sex was distinguishable in the downstream section were significantly different among sampling years with more males observed in 2007 ($\chi^2 = 8.062$, $df = 2$, $p < 0.05$) (Figure 2-6). Sex ratios of *G. geographica* for which sex was distinguishable in the upstream section were not significantly different among sampling years ($\chi^2 = 0.173$, $df = 2$, $p > 0.05$) (Figure 2-6).

Movement data from recapture histories in the downstream section suggest that 84% of the recaptured *G. geographica* moved less than 184 m and only 11% of recaptures had moved greater than 460 m. Movement data from recapture histories in the upstream section suggest that 76% of the recaptured *G. geographica* moved less than 184 m and only 11% of recaptures had moved greater than 460 m. The maximum distance moved by a *G. geographica* in the downstream study section was by a female turtle that moved 1,104 m downstream. The

maximum distance moved by a *G. geographica* in the upstream study section was by another female turtle that moved 3,703 m upstream.

A major assumption of this research is that the two turtle communities are distinct (i.e., no migration occurs between communities). Based on historical (Nickerson unpublished data, Pitt 2005) and recent movement estimates within NFWR, the two research sections are distant enough that natural migration is unlikely. Any natural migration attempted would be limited by a man-made boulder line placed between the two research sections. This boulder line was built to create a water retention area adjacent to a resort. If exchange between populations did occur, it would be possible to identify the origin of tagged individuals.

One confounding factor is human-facilitated migration because canoeists will occasionally capture and carry individuals for the length of their float. During this three-year study, only one tagged individual from upstream was found in the downstream section. This suggests that though canoeists may occasionally carry turtles downstream, it is either rare that this transportation happens or unlikely that turtles from the upstream section are deposited in the downstream section. In either scenario, exchange between populations remains extremely low and what does occur is likely unidirectional.

Similarly, unidirectional transport may occur with flooding. In 1970, flooding dislodged a large tree from within the downstream research section and deposited it outside of the research section (Nickerson et al. 2007). Despite this disturbance, many turtles were recaptured within the same or proximate areas in which they were originally captured (M. Nickerson personal communication). A flood in July 2007 that was large enough to submerge all but the very tops of the largest boulders (i.e., water rose approximately 1 meter in depth) did not appear to affect the distribution of *G. geographica* within NFWR as recaptures of turtles within their usual

capture sites after the flood were common. These data suggest that turtles have behavioral adaptations that counteract, diminish, or eliminate displacement associated with flooding.

Discussion

The results of this study indicate that turtle communities vary in composition, species richness, and heterogeneity in time and in different sections of a river. This variation corresponds with differences in abiotic factors between river sections and within each section through time.

Graptemys geographica was the numerically dominant species in both research sections and all sampling periods (Figure 2-3A and B). This result is consistent with patterns observed for other lotic systems, where river turtle fauna is dominated by *Graptemys* (Bury 1979, Moll and Moll 2004). No more than five species were ever observed in the downstream section in any given year (Figure 2-3A). However, the identity of species changed as certain rare species were observed in some years but not others (Figure 2-3A). Six species were observed in the upstream section in all years (Figure 2-3B), though this is not accurately reflected in Figure 2-3B for 2007 due to the failure to capture the regularly observed *A. spinifera*. The identity of species in the upstream section also varied as certain rare species were observed in some years but not others (Figure 2-3B). The failure to observe all rare species in all years may be a result of species being transient and not remaining in an area. Alternatively, rare species may not be observed in a given year due to the low probability of observing a numerically rare species.

Species richness, as determined by the rarefaction method, was higher in 1969 than in recent years in the downstream section (Figure 2-4A). The maximum difference in expected number of species among all years for any given sample size for the downstream section was between 0.07 – 0.87 (Figure 2-4A). Species richness within the upstream station was highly variable among years (Figure 2-4G). The maximum difference in expected number of species

among all years for any given sample size for the upstream section was between 0.97 – 2.24 (Figure 2-4G). If the 2007 rarefaction curve for the upstream section was corrected for the failure to capture any of the regularly observed *A. spinifera*, it would almost entirely overlap the 2006 curve (Figure 2-4H). The maximum difference in expected number of species among all years for any given sample size for the upstream section would then be between 0.07 – 1.39 (Figure 2-4H). The community in the upstream section typically had higher species richness than the downstream section in 2005 and 2006 (Figures 2-4C-D). Data collected in 2007 indicated that the downstream section had higher species richness for most sample sizes evaluated (Figure 2-4E). However, when the community composition in the upstream section was corrected for the failure to capture the regularly observed *A. spinifera*, the rarefaction curve for the community in the upstream section shifted upwards (Figure 2-4F). Species richness for the community in the upstream section then exceeded that of the downstream section for larger sample sizes (Figure 2-4F). These results indicated that the upstream section contained more species than the downstream section and this pattern was reflected especially at larger sample sizes. Comparison of the species composition of each section indicated that the primary differences in species richness was due to the upstream section having a small population of *A. spinifera*, a species observed only once in the downstream section in recent years (Figures 2-3A and B). In addition, one *M. temminckii* was captured three times in the upstream section, once in 2006 and twice in 2007 (Figure 2-3B). *Macrochelys temminckii* was never observed in the downstream section in previous or recent surveys (Figure 2-3A).

Heterogeneity, which takes into account both species richness and evenness, was higher for the downstream section in 2005 to 2007 than for either the upstream section in 2005 to 2007 or the downstream section in 1969 (Table 2-1). These results are indicative of the increased species

evenness associated with an increase in *S. odoratus* and *T. s. elegans* observed in the downstream section in 2005 to 2007 (Figure 2-3A). Heterogeneity varied little within each site in 2005 to 2007 (Table 2-1). However, heterogeneity of the turtle community in the upstream section was higher in 2005 than in subsequent years (Table 2-1). This result corresponds with the higher species richness (Figure 2-4G) but also with a more even species composition in 2005 in the upstream community than in the following years (Figure 2-3B). The downstream community in 2005 appeared to be more even as well, but fewer overall species were found (i.e., species richness was lower than in other years) (Figures 2-3A and 2-4A) so the heterogeneity measure remained fairly constant (Table 2-1).

Overall, the turtle community in the upstream section had higher species richness, but lower heterogeneity than that of the downstream section. These results indicate that the upstream section contains more rare turtle species than the downstream section. Interestingly, heterogeneity measures from the downstream section in 1969 were more similar to those from the upstream section in recent years (Table 2-1). This is indicative of the lower evenness of the downstream section in 1969 as richness is more similar to that of the same section in recent years (Figures 2-4A and B).

All species except *M. temminckii* were observed basking at least once during the study period (Table 2-2). Basking is essential for thermoregulation, digestion, maintenance of integumentary health, vitamin D synthesis, and parasite removal (Hutchison 1979, Vogt 1979, Hart 1983, Saumure and Livingston 1994, Vogt and Benitez 1997). Many species of turtles bask, but this behavior is most often associated with turtles within the family Emydidae (Boyer 1965), such as *G. geographica* and *T. s. elegans*. Few conclusions can be drawn regarding basking behavior of rare species in NFWR, except that it was observed (Table 2-2). Measures of

niche breadth indicated that *G. geographica* used fewer types of basking substrates in the downstream section in 1969 to 1972 and in the upstream section than in the downstream section in recent years (Table 2-3). In 1969 to 1972, *G. geographica* were most commonly observed basking on rocks and logs (Table 2-2). In the upstream section in 2005 to 2007, *G. geographica* frequently used branches, logs, and rocks as basking sites (Table 2-2). In 2005 to 2007, *G. geographica* in the downstream section frequently used four types of basking substrates: branches, vegetation, logs, and rocks. Use of particular basking substrates is likely linked with the relative abundances of basking substrates. Quantifying basking substrates was attempted initially in the downstream section, but was quickly abandoned due to the inherent difficulty of quantifying ephemeral substrates. For example, branches would get dislodged and swept downstream and vegetation increased rapidly throughout the summer months. Despite this limitation, preliminary measurements indicated there was a significantly higher amount of aquatic vegetation in the downstream section in recent years than in previous years or in the upstream section. This difference in vegetation abundance corresponds with the increased use of vegetation as a basking substrate by *G. geographica* (Table 2-2). *Trachemys scripta elegans* were also frequently observed basking on vegetation in the downstream section in 2005 to 2007 (Table 2-2). Niche breadth analysis indicated that *T. s. elegans* commonly used two types of basking substrates (Table 2-3), but the use of logs (N = 11) was far surpassed by the use of vegetation (N = 35) (Table 2-2). *Sternotherus odoratus* had the narrowest niche breadth and used only one type of basking substrate frequently (Table 2-3): vegetation (Table 2-2). In summary, *G. geographica* had the widest niche breadth (Table 2-3), a trait indicative of a generalist for the characteristic in question (Krebs 1989). *Sternotherus odoratus* had the narrowest niche breadth (Table 2-3), which indicates a basking habitat specialist (Krebs 1989). I

hypothesize that niche breadth and use of different basking habitats may be more indicative of physiological needs and relative competitive ability. Basking is most highly developed in emydid turtles (Boyer 1965), which indicates the relative importance of this behavior to this taxon. Therefore, individuals may exploit less preferred basking habitats to undergo this essential behavior if preferred basking substrates are limited. Pitt (2005) noted that fewer emergent boulders were present in 2004 than in previous years. This observation suggests that fewer basking substrates were available onto which turtles could fully emerge from the water. This observation supports the hypothesis that *G. geographica* were increasing their basking niche breadth in response to fewer preferred basking substrates. This hypothesis corresponds with the prediction that niche breadth should increase as resources decrease (Pianka 1976).

Measures of niche overlap indicate significant overlap in basking habitat use among species (Table 2-4). High niche overlap can be indicative of shared resource utilization and lack of competition or intense competition that has not yet led to resource partitioning (Pianka 1976). In this system, I suspect that competition is responsible for the observed patterns of basking habitat use, with *G. geographica* being a better competitor than *T. s. elegans* and *S. odoratus*. *Trachemys scripta elegans* were not observed in the research section in 1969 (Figure 2-3A, Table 2-2). Subsequent surveys starting in 1980 indicated a small population of *T. s. elegans* had become established in the downstream section of NFWR (Pitt 2005). *Trachemys scripta elegans* appearance in the research section corresponded with a decline in the *G. geographica* population, suggesting that *T. s. elegans* were able to exploit the newly available habitat (Pitt 2005). The *G. geographica* population failed to rebound and basking habitat, in the form of vegetation, increased in abundance (Pitt 2005). Because *T. s. elegans* is a highly adaptable generalist species (Vogt and Benitez 1997, Webb 1961), changes in community composition and habitat allowed

the *T. s. elegans* population to persist in the downstream section of NFWR through 2007. This hypothesis is supported by the disproportionate use of vegetation by *T. s. elegans* in recent years (Table 2-2).

A similar pattern of niche exploitation is suspected for *S. odoratus*. Data from 1969 – 1972 indicate a small population of *S. odoratus* that was typically observed basking in live trees, logs, and branches (Table 2-2). More recently, the *S. odoratus* population has become a major portion of the turtle community in the downstream section of NFWR (Figure 2-3A). All but four of the 130 *S. odoratus* observed basking were associated with vegetation (Table 2-2). I hypothesize that *S. odoratus* were able to expand their population within NFWR due to the large expanses of emergent vegetation observed in the downstream section in recent years. In addition to availability in basking habitat, emergent vegetation was associated with muddy, silty substrates, a typical habitat of *S. odoratus* (Kingsbury 1993). *Sternotherus odoratus* are typically associated with more lentic habitats with slow or no current and soft bottom substrates (Ernst et al. 1994). *Sternotherus odoratus* within NFWR appear to be closely associated with water lilies (*Nymphaea* spp.) and algal mats situated on emergent aquatic vegetation growing from a soft sediment substrate. With appearance of algal mats in the downstream section since 1980 (Pitt 2005), and the relatively large area that they cover compared to the upstream section, it is likely that the downstream section contains more suitable habitat for *S. odoratus* than it did in previous studies and when compared to the upstream section.

These conclusions are based on the assumption that *G. geographica* prefer basking sites other than vegetation, including logs, branches, and rocks. Pitt (2005) concluded that *G. geographica* preferred highly-branched, felled trees near deeper water. Flaherty and Bider (1984) found that *G. geographica* in an area with excess basking habitats preferred basking

substrates that were long, narrow, far from land and aquatic vegetation, and in deep water. Flaherty and Bider's (1984) results suggest that *G. geographica* avoid aquatic vegetation when other types of potential basking substrates are present. *Graptemys geographica* may prefer branches, logs, and rocks as these substrates allow the turtles to remove their entire bodies from the water. This extrication from the water allows for drying of the integument (Cagle 1950) and parasite removal as leeches desiccate in the sun (Boyer 1965) or are removed by birds (Vogt 1979). Warmer body temperatures within a particular range are beneficial as they are associated with enhanced physiological function including digestion (Cagle 1950, Hutchison 1979).

The *G. geographica* populations within the two research sections were not significantly different in size. This result is surprising as the downstream section encompasses a significantly larger aquatic area and volume than the upstream section. I predict that a larger area of a given habitat would support more resources, such as basking sites, than a smaller area of the same habitat. More resources should increase the carrying capacity of a habitat so I would predict more turtles would be found in a larger area. Pitt (2005) determined that the *G. geographica* population in the downstream section had declined from 1969 levels and remained steady at the declined value due to life history trait limitations, interspecific interactions, and habitat characteristics. Estimated *G. geographica* population sizes increased among sampling years in 2005 to 2007 in both research sections (Table 2-8), but only the population estimates from the upstream section were significantly different. The observed differences in *G. geographica* population sizes correspond with increased recruitment in 2006 and 2007 (Figures 2-5A and B).

No significant differences between *G. geographica* plastron lengths, partitioned by sex, were observed between populations in each research section (Table 2-9). Sex ratios of *G. geographica* for which sex could be distinguished visually did not differ from 1:1 (male:female)

for any year or station (Figure 2-6). These data provide evidence that the *G. geographica* populations within the upstream and downstream sections in 2005 to 2007 were structured similarly.

Typically, a larger area contains more species and perhaps larger populations than a smaller area (Groom 2006). Additionally, larger areas often contain a higher diversity of microhabitats than do smaller areas (Pluto and Bellis 1988, Dunning et al. 2006). Based on the premise that larger areas can support more species than smaller areas, I would expect that more species would be observed in the downstream section as it has a larger aquatic area and volume. However, the opposite pattern was observed. When viewed in the light of the habitat differences between the two research sections, the results may not be counterintuitive.

Water temperatures were significantly different between the two research sections. Because turtles are ectothermic, water temperature can strongly influence body temperature (Boyer 1965, Schuett and Gatten 1980, Brown et al. 1994). Turtles may move to and among areas of favorable temperatures in their aquatic habitats (Schuett and Gatten 1980, Thornhill 1982, Moll and Moll 2004). As a result, some species may select habitats with higher water temperatures and avoid cooler thermal regimes. Some species, such as *Graptemys* and *Trachemys*, further regulate their body temperatures by basking (Boyer 1965, Gatten 1974, Schuett and Gatten 1980, Spotila et al. 1984, Cadi and Joly 2003) and can inhabit a broader range of temperatures as long as sufficient basking habitat is available. Therefore, basking allows these species to increase their distribution into cooler water bodies that would otherwise not have favorable thermal regimes. The mean water temperature in the downstream section observed in the summer months (i.e., June, July, and August) was 18.7 °C. Low temperatures may deter or prohibit the use of the downstream section by some species because temperature

strongly affects physiological function in turtles (Cagle 1946, Boyer 1965, Gatten 1974, Parmenter 1980, Thornhill 1982, Brown and Brooks 1991, Frazer et al. 1993, Brown et al. 1994, Cadi and Joly 2003, Cadi and Joly 2004).

The upstream research section is less impacted by humans. If turtles prefer less impacted habitats, the differences observed between the turtle communities and populations are expected. The upstream section is surrounded by Mark Twain National Forest land so the majority of the riparian zone and beyond is forested and undeveloped (Bryant Watershed Project, Inc. 2008). Along the entire upstream research section, the only clearing is associated with the national forest campground and boat ramp located at the upstream boundary of the research section. In contrast, there are five cleared areas surrounding portions of the downstream section (Pitt 2005). The intact forest and riparian zones, such as those characterizing the upstream section, are known to prevent excess sediment runoff from surrounding areas during rain events (Gilliam 1994). Additionally, the lack of development surrounding the upstream section prevents common practices associated with development, such as applications of fertilizers and pesticides, which occurs in cleared and developed areas along other portions of the river. Lastly, private residences along NFWR are often located close to the river's edge, which increases the risk of septic systems seeping their contents into the river. This hypothesis is supported by the observed patterns of *E. coli* contamination within NFWR (Figure 2-2). Only the first station within the upstream research section had *E. coli* levels that exceeded concentrations deemed safe for full body contact by MDNR (Figure 2-2). In contrast, all areas sampled within the downstream section had *E. coli* levels that exceeded concentrations deemed safe for full body contact in at least one sampling event during the summer (Figure 2-2).

In addition to more riparian development and higher bacterial loads, the downstream section also contains larger amounts of aquatic vegetation, including extensive algal mats which were not observed in surveys preceding 2004 (Pitt 2005). Long, fibrous submerged algae (*Cladophora* spp.) were observed in surveys preceding 2004, but were less plentiful and did not bloom for as long a time period (Nickerson personal communication). These observations suggest that nutrient-loading is occurring in the downstream section as algal blooms are often associated with nutrient-loading (Groom and Vynne 2006). Previous studies confirm that nutrient-loading has occurred in NFWR (M. Solis personal communication).

Further evidence of degraded habitat quality in the downstream research section is illustrated by the comparison of the upstream section's community composition with the community composition of the downstream section observed in 1969 (Figure 2-3A). Comparison of these data indicates that the present day community composition of the upstream section most closely resembles that of the downstream section in 1969. These similarities may arise because the upstream and downstream sections were relatively un-impacted by people in 2005 to 2007 and 1969, respectively. Community composition changes observed within an impacted river in Illinois illustrated a change from more specialized to more generalized turtle species (Moll 1977, 2006). The higher relative proportion of *T. s. elegans* and *S. odoratus* (i.e., generalist species) observed in the downstream section may be symptomatic of a more heavily impacted habitat.

Overall, both river sections and the associated springs are impacted to some extent. This conclusion is well illustrated by the bacterial analyses conducted within NFWR and its associated springs (Figures 2-1 and 2-2). All sites sampled exceeded total coliform limits deemed safe for full body contact by the MDNR in at least one sampling event during the

summer (Figure 2-1). Furthermore, all springs, downstream sampling sites, and one upstream sampling site had *E. coli* values that exceeded the limits deemed safe for full body contact (Figure 2-2). Because the Ozark Plateau is composed of karst geology (The Nature Conservancy 2003), these results indicate that not only are stormwater runoff and septic systems potentially directly contaminating water bodies, but the groundwater itself is contaminated. These results do not bode well for wildlife or humans inhabiting these areas, especially if these results are foreshadowing high concentrations of other contaminants, such as pesticides and metals. Previous studies have confirmed the presence of pesticides in NFWR (MDC 2005).

Conclusions

The North Fork of White River, Ozark County, Missouri, supports a diverse turtle assemblage predominated by *Graptemys geographica*. Turtle communities in NFWR varied in composition, species richness, and heterogeneity through time and in close sections of a river. The downstream turtle community shifted from an assemblage of one common species and several rare species to a grouping of several common species and a few rare species. The turtle community in previous years was most similar to that of the upstream section in recent years. The observed variation among turtle communities corresponded with spatial and temporal differences in abiotic factors. Based on these results, I conclude that factors such as spring effluents, riparian development, water quality, and algal blooms are disproportionately affecting different areas and associated turtle communities within this river.

These results support the hypothesis that turtle communities can vary in composition, species richness, and heterogeneity through time and in relatively close sections of a river with a natural thermal gradient. Variation in turtle communities and populations corresponded with differences in abiotic factors between river sections and within a section through time. Changes in community composition can result in increased biotic interactions, including competition. The

observed variation among communities and the suspected overwhelming influence of abiotic factors on the turtle communities lends support to nonequilibrium community theories.

Nonequilibrium community theories integrate the idea that the environment (i.e., abiotic factors) strongly influences organisms and is perpetually changing (Chesson and Case 1986). As a result of these changes, the populations and communities that inhabit the environment vary (Davis 1986, Cody 1996).

The human population is increasing rapidly (Cohen 1995) and most rivers have undergone massive alterations due to the water and land needs of humans (Benke 1990, Riccardi and Rasmussen 1999). As development alters land and water bodies, it is imperative to understand how these alterations will impact wildlife. With long-term studies that illustrate spatial and temporal variation in communities and populations, it will be possible to discern the cause of the variability (Cody 1996). With such data, conservation and management decisions will be based on sound science rather than guesswork.

Turtle populations are declining worldwide (Smith 1979, Moll 1986, Kuchling 1988, Ernst et al. 1994, Buhlmann and Gibbons 1997, Gibbons 1997, Haitao 2000, van Dijk et al. 2000, Moll and Moll 2004), but studies, such as this one, that increase knowledge of the ecology, population status, and community composition of turtle species and assemblages (Moll 1990, Ernst et al. 1994, Moll and Moll 2004) increase the possibility of garnering political, social, and financial support for conservation of imperiled chelonians (Gibbons 1997).

This study provides new insights on spatial and temporal variation of river turtle communities and populations and provides necessary information for future conservation actions.

Table 2-1. Heterogeneity measures for turtle communities in the North Fork of White River, Ozark County, Missouri.

Sampling year	Simpson's Index of Diversity (modified for a finite population)	Reciprocal of Simpson's Index of Diversity
Downstream section		
1969	0.286	1.398
2005	0.596	2.445
2006	0.597	2.456
2007	0.537	2.143
Upstream section		
2005	0.379	1.599
2006	0.167	1.198
2007	0.094	1.102
2007 + 5 <i>Apalone spinifera</i>	0.161	1.190

Table 2-2. Summary of turtle behavior and basking substrate use prior to capture in the North Fork of White River, Ozark County, Missouri. All capture and recapture events for which data are available are included.

	# Submerged	# Basking							
		Live tree	Log	Branch	Rock	Vegetation	Freely-floating veg. debris	Bank	Unspecified substrate
Downstream section									
1969 - 1972									
<i>Apalone spinifera</i>	1	0	0	0	0	0	0	0	0
<i>Chelydra serpentina</i>	1	0	1	0	0	0	1	0	0
<i>Graptemys geographica</i>	40	1	28	6	36	3	3	3	17
<i>Macrochelys temminckii</i>	None captured								
<i>Pseudemys concinna</i>	None captured								
<i>Sternotherus odoratus</i>	3	4	5	3	0	0	0	0	2
<i>Trachemys scripta elegans</i>	None captured								
2005 - 2007									
<i>Apalone spinifera</i>	0	0	0	0	0	1	0	0	0
<i>Chelydra serpentina</i>	7	0	1	0	0	2	0	0	0
<i>Graptemys geographica</i>	49	0	56	92	52	67	0	0	1
<i>Macrochelys temminckii</i>	None captured								
<i>Pseudemys concinna</i>	0	0	1	0	0	1	0	0	0
<i>Sternotherus odoratus</i>	3	0	2	2	0	126	0	0	0
<i>Trachemys scripta elegans</i>	20	0	11	9	5	35	2	1	2
Upstream section									
2005 - 2007									
<i>Apalone spinifera</i>	2	0	1	0	0	0	0	0	0
<i>Chelydra serpentina</i>	2	0	0	0	0	0	0	0	0
<i>Graptemys geographica</i>	169	3	51	83	30	13	2	0	1
<i>Macrochelys temminckii</i>	3	0	0	0	0	0	0	0	0
<i>Pseudemys concinna</i>	1	0	0	0	1	0	0	0	0
<i>Sternotherus odoratus</i>	2	0	0	1	0	1	0	0	0
<i>Trachemys scripta elegans</i>	16	0	2	0	2	1	0	0	0

Table 2-3. Basking substrate niche breadth for turtle species in the North Fork of White River, Ozark County, Missouri.

	Levins' Standardized Measure	# of frequently used basking substrates
Downstream section		
1969 - 1972		
<i>Graptemys geographica</i>	0.331	2
<i>Sternotherus odoratus</i>	0.313	3
2005 - 2007		
<i>Graptemys geographica</i>	0.466	4
<i>Sternotherus odoratus</i>	0.011	1
<i>Trachemys scripta elegans</i>	0.212	2
Upstream section		
2005 - 2007		
<i>Graptemys geographica</i>	0.356	3

Table 2-4. Pianka's niche overlap index for turtle communities in the North Fork of White River, Ozark County, Missouri. Data for the downstream section (DS) in 1969 – 1972 and the upstream section (US) are representative of the number of species observed basking. Dashes indicate lack of data for species or overlap values that were represented elsewhere in the table.

	<i>Apalone spinifera</i>	<i>Chelydra serpentina</i>	<i>Graptemys geographica</i>	<i>Pseudemys concinna</i>	<i>Sternotherus odoratus</i>	<i>Trachemys scripta elegans</i>
DS 1969 - 72						
<i>A. spinifera</i>	---	---	---	---	---	---
<i>C. serpentina</i>	---	---	0.4734	---	0.500	---
<i>G. geographica</i>	---	---	---	---	0.4948	---
<i>P. concinna</i>	---	---	---	---	---	---
<i>S. odoratus</i>	---	---	---	---	---	---
<i>T. s. elegans</i>	---	---	---	---	---	---
DS 2005 - 07						
<i>A. spinifera</i>	---	0.8944	0.4887	0.7071	0.9997	0.9169
<i>C. serpentina</i>	---	---	0.6198	0.9487	0.9013	0.949
<i>G. geographica</i>	---	---	---	0.6344	0.5057	0.7738
<i>P. concinna</i>	---	---	---	---	0.7181	0.8521
<i>S. odoratus</i>	---	---	---	---	---	0.9250
<i>T. s. elegans</i>	---	---	---	---	---	---
US 2005 - 07						
<i>A. spinifera</i>	---	---	0.4961	0	0	0.6667
<i>C. serpentina</i>	---	---	---	---	---	---
<i>G. geographica</i>	---	---	---	0.2918	0.6603	0.5674
<i>P. concinna</i>	---	---	---	---	0	0.6667
<i>S. odoratus</i>	---	---	---	---	---	0.2357
<i>T. s. elegans</i>	---	---	---	---	---	---

Table 2-5. Mean water depth in which the turtles or their basking substrates were located prior to capture in the North Fork of White River, Ozark County, Missouri. All capture and recapture events for which data were available were included.

	N	Mean water depth (m)	Range (m)	Standard deviation
Downstream section				
1969 - 1972				
<i>Apalone spinifera</i>	1	0.61	---	---
<i>Chelydra serpentina</i>	No data			
<i>Graptemys geographica</i>	49	0.67	0.30 – 1.30	0.2256
<i>Macrochelys temminckii</i>	None captured			
<i>Pseudemys concinna</i>	None captured			
<i>Sternotherus odoratus</i>	3	1.07	0.91 – 1.22	0.1550
<i>Trachemys scripta elegans</i>	None captured			
2005 - 2007				
<i>Apalone spinifera</i>	1	0.30	---	---
<i>Chelydra serpentina</i>	9	1.03	0.45 – 2.00	0.5483
<i>Graptemys geographica</i>	257	0.74	0.10 – 2.00	0.3714
<i>Macrochelys temminckii</i>	None captured			
<i>Pseudemys concinna</i>	1	1.10	---	---
<i>Sternotherus odoratus</i>	77	0.76	0.27 – 1.50	0.2310
<i>Trachemys scripta elegans</i>	66	0.71	0.05 – 1.75	0.3224
Upstream section				
2005 - 2007				
<i>Apalone spinifera</i>	1	0.35	---	---
<i>Chelydra serpentina</i>	No data			
<i>Graptemys geographica</i>	278	0.69	0.06 – 2.00	0.3288
<i>Macrochelys temminckii</i>	3	1.20	0.80 – 1.50	0.3606
<i>Pseudemys concinna</i>	2	0.85	0.40 – 1.30	0.6364
<i>Sternotherus odoratus</i>	4	0.56	0.40 – 0.75	0.1493
<i>Trachemys scripta elegans</i>	11	0.80	0.05 – 1.50	0.4860

Table 2-6. Mean water depth in which the turtles or basking substrates were located prior to capture in the North Fork of White River, Ozark County, Missouri. All capture and recapture events for which data were available were included.

	Sex	N	Mean water depth (m)	Range (m)	Standard deviation
Downstream section					
1969 - 1972					
<i>Graptemys geographica</i>	Indeterminate	14	0.74	0.30 – 1.30	0.3051
	Female	16	0.58	0.30 – 0.91	0.1729
	Male	19	0.66	0.30 – 1.07	0.1855
2005 - 2007					
<i>Graptemys geographica</i>	Indeterminate	81	0.59	0.10 – 2.00	0.3238
	Female	83	0.72	0.15 – 2.00	0.3654
	Male	95	0.88	0.20 – 2.00	0.3625
<i>Sternotherus odoratus</i>	Indeterminate	Not included in analysis due to very small N (N = 5)			
	Female	45	0.78	0.40 – 1.50	0.2247
	Male	26	0.75	0.40 – 1.20	0.2278
<i>Trachemys scripta elegans</i>	Indeterminate	32	0.60	0.05 – 1.00	0.2685
	Female	22	0.87	0.10 – 1.75	0.3670
	Male	12	0.71	0.40 – 1.20	0.2577
Upstream section					
2005 - 2007					
<i>Graptemys geographica</i>	Indeterminate	116	0.54	0.60 – 1.25	0.2555
	Female	83	0.79	0.10 – 2.00	0.3648
	Male	87	0.81	0.15 – 1.50	0.3337

Table 2-7. Tukey's post-hoc procedure results for difference in mean water depth use by *Graptemys geographica* (Gg), *Sternotherus odoratus* (So), and *Trachemys scripta elegans* (Tse) partitioned by sex [I = indeterminate sex (i.e., hatchlings, posthatchlings), F = females, M = males] in the downstream section of the North Fork of White River, Ozark County, Missouri in 2005 to 2007. Significant differences are indicated by an asterisk (*). All capture and recapture events for which data were available were included.

	Gg I	Gg F	Gg M	So F	So M	Tse I	Tse F	Tse M
Gg I	---	0.000*	0.000*	0.000*	0.019*	0.949	0.000*	0.506
Gg F	---	---	1.000	1.000	0.999	0.055	0.926	0.991
Gg M	---	---	---	0.999	0.987	0.017*	0.984	0.962
So F	---	---	---	---	1.000	0.157	0.925	0.997
So M	---	---	---	---	---	0.547	0.839	1.000
Tse I	---	---	---	---	---	---	0.022*	0.958
Tse F	---	---	---	---	---	---	---	0.790
Tse M	---	---	---	---	---	---	---	---

Table 2-8. Schumacher-Eschmeyer population size and corresponding density estimates of *Graptemys geographica* in 2005, 2006, and 2007 in the North Fork of White River, Ozark County, Missouri. Density estimates were based on area calculated from mean stream width and total sample length for each section.

Sampling year	Estimated population size	95% confidence interval	Estimated density
Downstream section			
2005	114	80-198	1 turtle/ 1751 m ²
2006	270	172-623	1 turtle/ 739 m ²
2007	308	204-621	1 turtle/ 648 m ²
Upstream section			
2005	115	92-154	1 turtle/ 1136 m ²
2006	304	189-779	1 turtle/ 430 m ²
2007	578	317-3231	1 turtle/ 226 m ²

Table 2-9. Mean plastron lengths (PL) of *Graptemys geographica* in 2005, 2006, and 2007 in the North Fork of White River, Ozark County, Missouri. N represents the sample size.

Sampling year	Sex	N	Mean PL (cm)	Range (cm)	Standard deviation
Downstream					
2005	Male	14	7.8	6.7 – 9.4	0.8565
	Female	23	13.0	6.0 – 19.6	5.7112
2006	Male	24	7.3	5.5 – 8.8	1.0336
	Female	34	12.7	5.0 – 19.6	5.9300
2007	Male	48	7.5	5.3 – 9.6	0.9492
	Female	30	14.3	5.1 – 19.5	5.5940
Upstream					
2005	Male	24	7.8	5.1 – 10.2	1.3189
	Female	20	11.2	5.6 – 19.5	4.7520
2006	Male	39	7.5	6.0 – 10.2	0.8901
	Female	38	13.3	5.1 – 20.2	5.4520
2007	Male	32	7.2	5.4 – 9.2	1.0488
	Female	29	12.6	4.3 – 20.5	5.0531

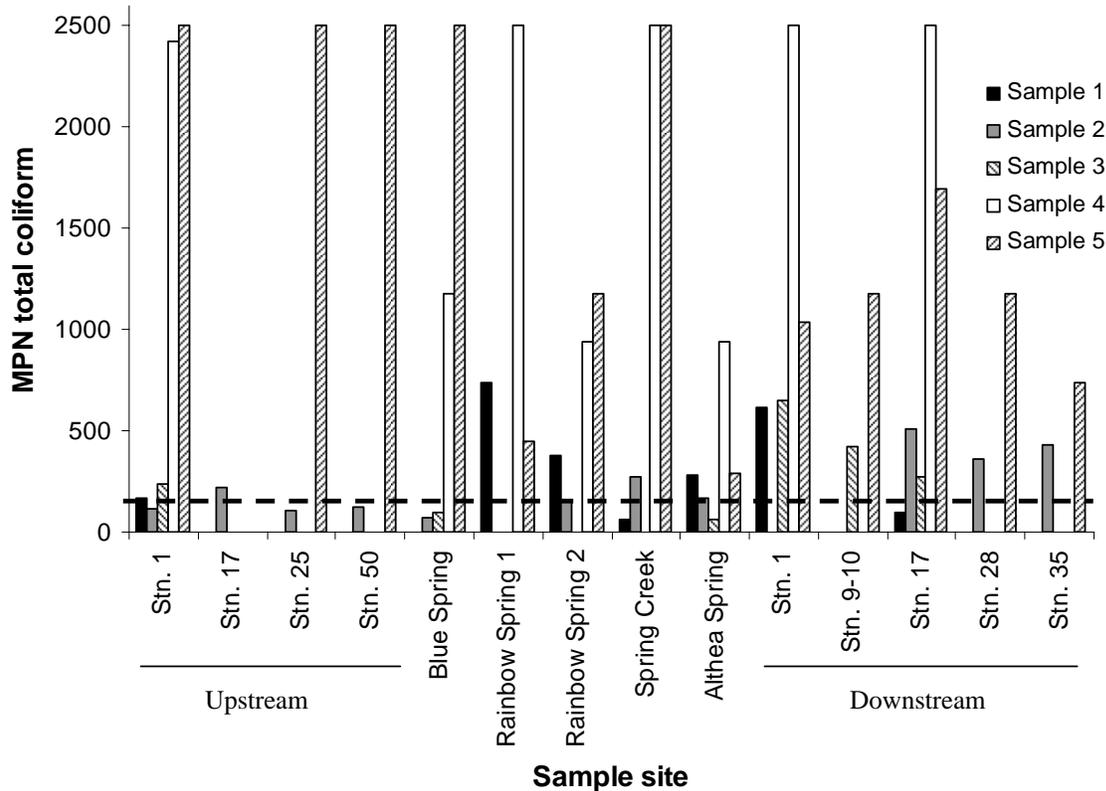


Figure 2-1. Total coliform bacteria content observed in the North Fork of White River, Ozark County, Missouri. “Upstream” and “downstream” indicate stations within the upstream and downstream research sections, respectively. Samples 1, 2, 3, 4, and 5 were collected during the third and fourth week of June, first and last week of July, and first week of August 2007, respectively. Samples were not collected at each site during each sampling period due to processing constraints. Sites for which no data were available lack values. “MPN” represents the most probable number of colony-forming units per 100 mL of water. The dashed line indicates the threshold total coliform bacteria concentration (200 MPN) deemed safe for full body contact by the Missouri Department of Natural Resources (MDNR) (2005). Values depicted equal to 2500 MPN represent MPN values > 2,424 rather than real values.

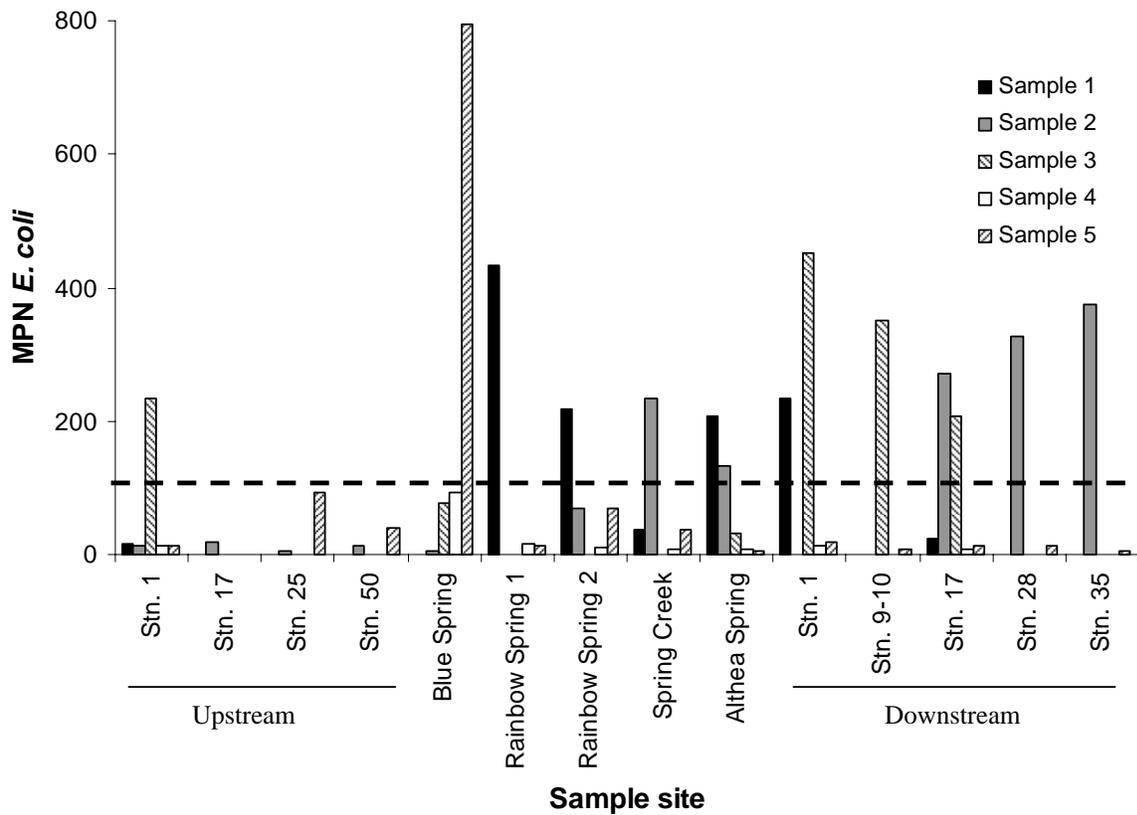


Figure 2-2. *Escherichia coli* content observed in the North Fork of White River, Ozark County, Missouri. “Upstream” and “downstream” indicate stations within the upstream and downstream research sections, respectively. Samples 1, 2, 3, 4, and 5 were collected during the third and fourth week of June, first and last week of July, and first week of August 2007, respectively. Samples were not collected at each site during each sampling period due to processing constraints. Sites for which no data were available lack values. “MPN” represents the most probable number of colony-forming units per 100 mL of water. The dashed line indicates the threshold *E. coli* concentration (126 MPN) deemed safe for full body contact by the Missouri Department of Natural Resources (MDNR) (2005). Values depicted equal to 1 MPN represent MPN values < 3 rather than real values.

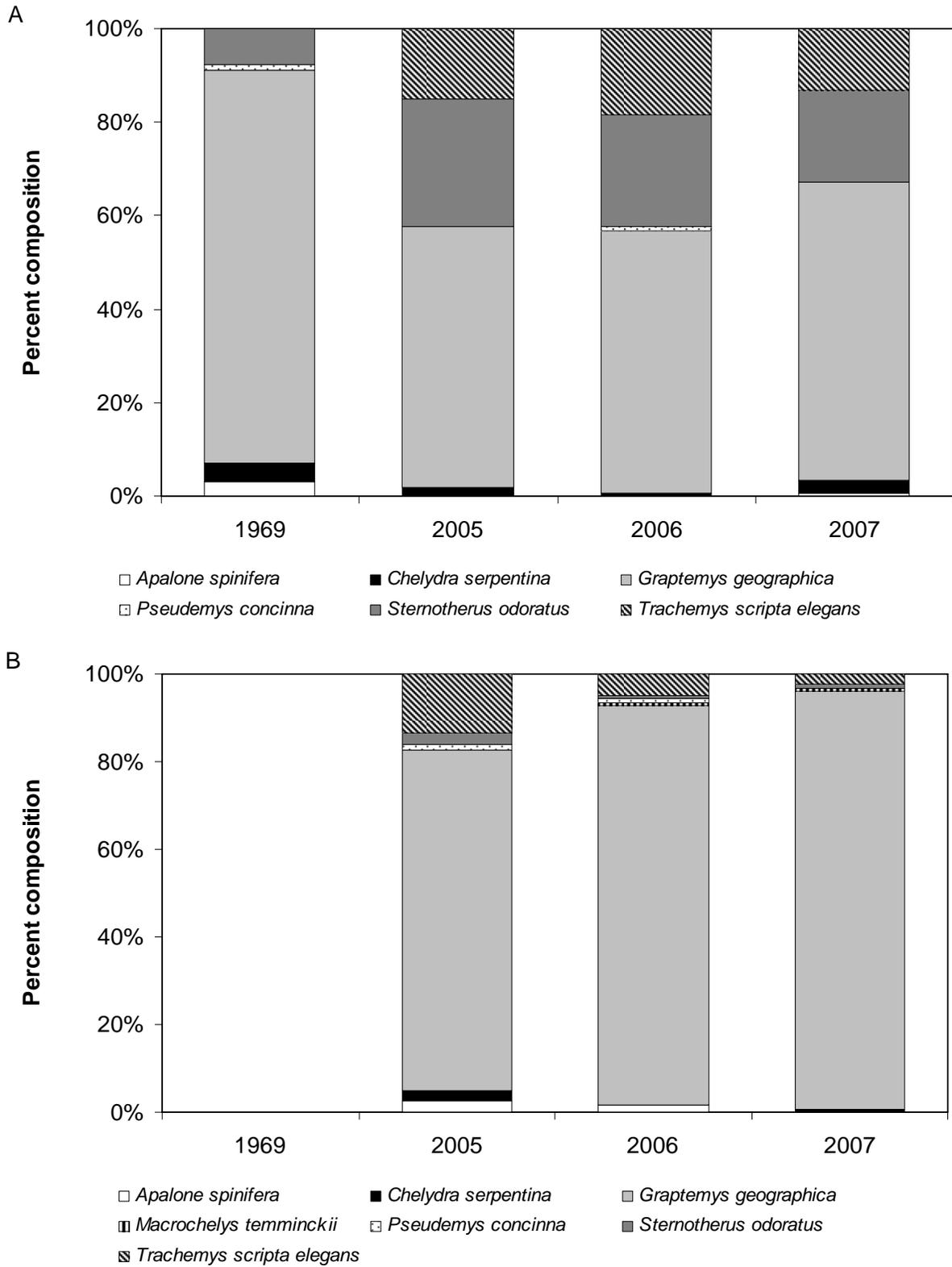


Figure 2-3. Turtle community structure in the (A) downstream and (B) upstream sections of the North Fork of White River, Ozark County, Missouri. No data were available for the upstream section in 1969.

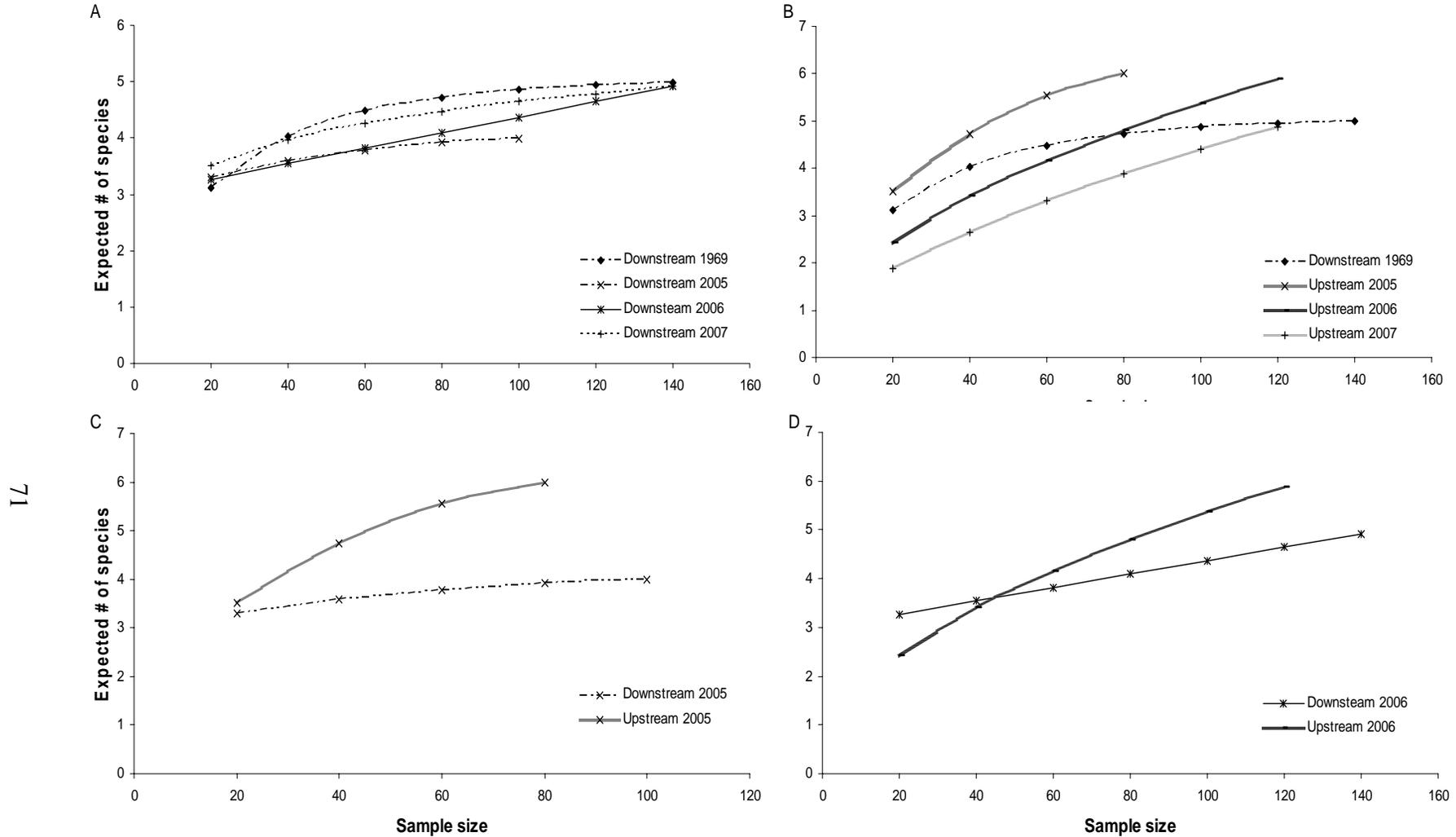


Figure 2-4. Rarefaction curves for the North Fork of White River, Ozark County, Missouri, turtle communities in the (A) downstream section (*DS*) in years 1969 and 2005, 2006, and 2007, (B) *DS* in 1969 and the upstream section (*US*) in 2005, 2006, and 2007, (C) *DS* and *US* in 2005, (D) *DS* and *US* in 2006, (E) *DS* and *US* in 2007, (F) *DS* and *US* in 2007 with an estimate of 5 *Apalone spinifera* added to the *US*'s species count, (G) *US* in 2005, 2006, and 2007, and (H) *US* in 2005, 2006, and 2007 with an estimate of 5 *A. spinifera* added to the *US*'s species count.

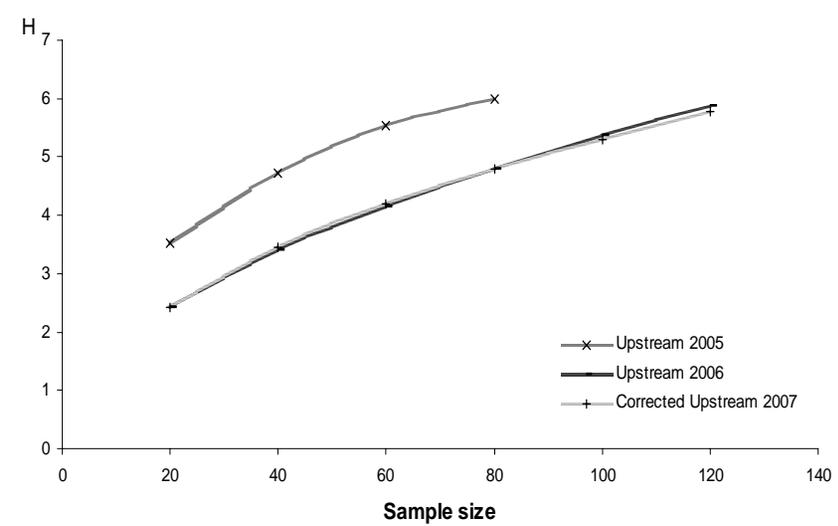
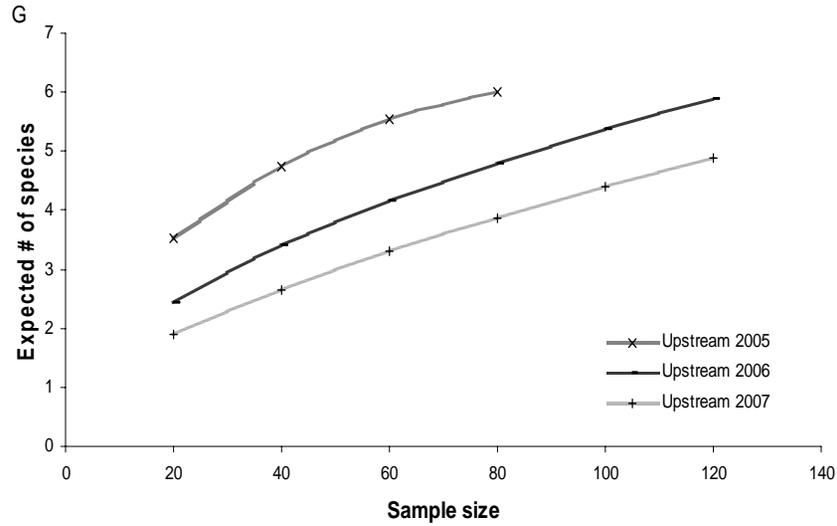
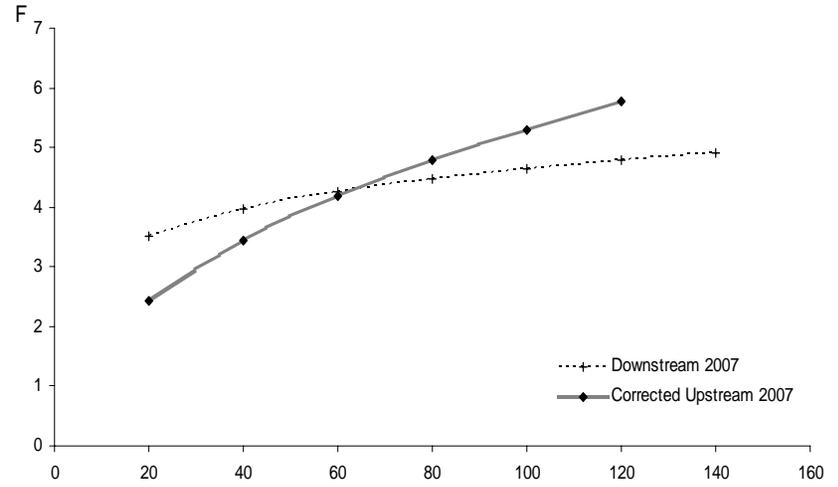
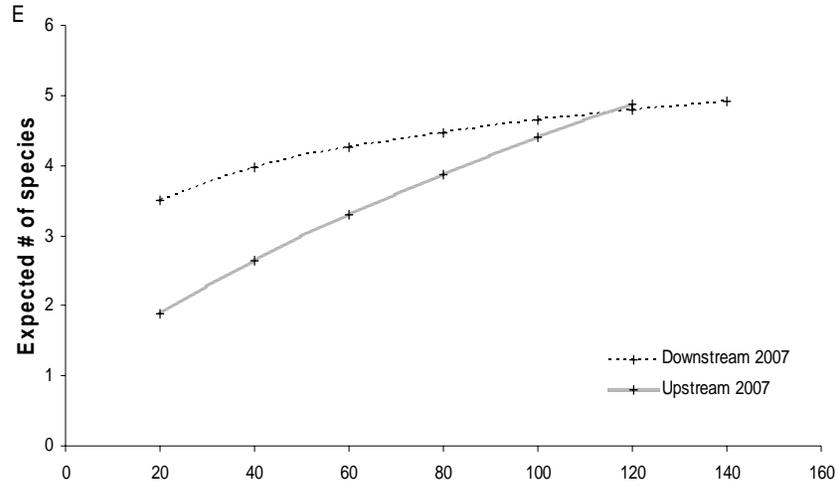


Figure 2-4. Continued.

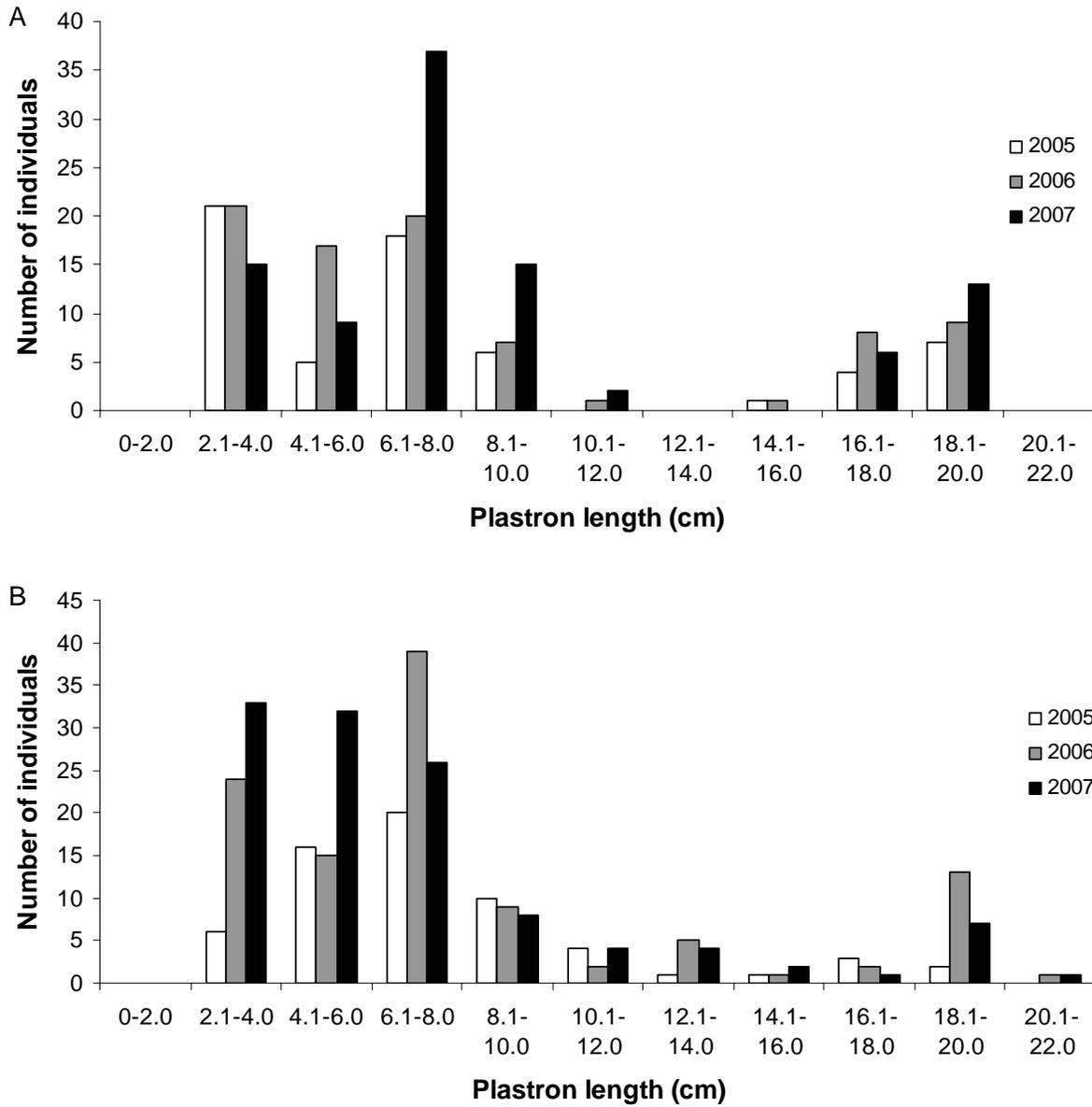


Figure 2-5. Size distribution of *Graptemys geographica* in the (A) downstream and (B) upstream sections of the North Fork of White River, Ozark County, Missouri (Downstream: 2005: n = 62, 2006: n = 84, 2007: n = 97; Upstream: 2005: n = 63, 2006: n = 111, 2007: n = 118). Note: Individuals with PL > 12 cm are all females.

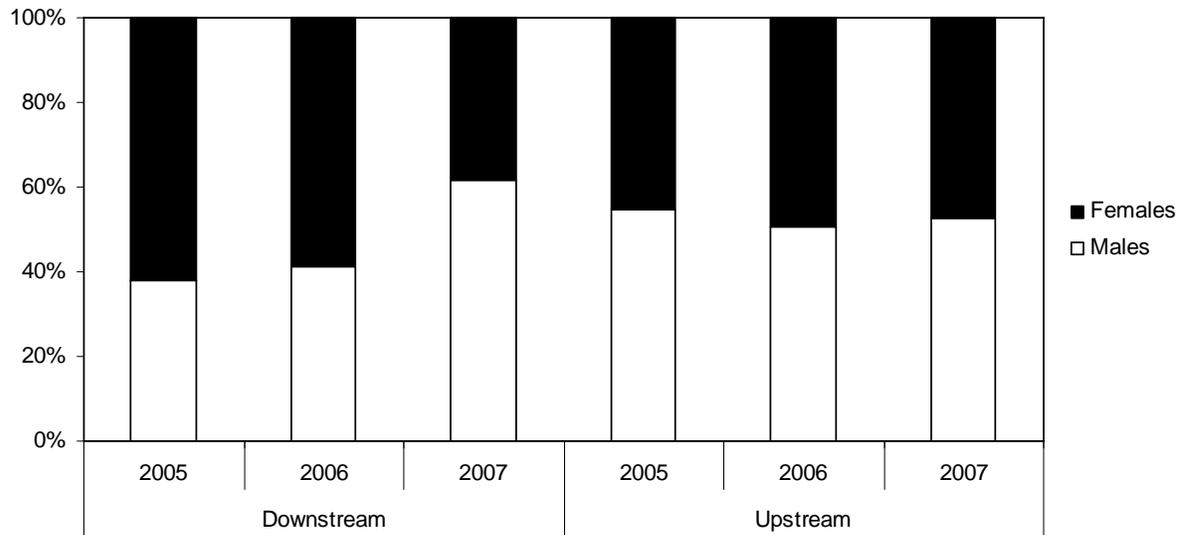


Figure 2-6. Sex ratios of mature *Graptemys geographica* in the North Fork of White River, Ozark County, Missouri (Downstream: 2005: n = 37, 2006: n = 58, 2007: n = 78; Upstream: 2005: n = 44, 2006: n = 77, 2007: n = 61).

CHAPTER 3
COMPARISON OF INSTANTANEOUS GROWTH RATES OF TEMPORALLY AND
SPATIALLY DISTINCT *Graptemys geographica* POPULATIONS INHABITING A RIVER
WITH A NATURALLY GENERATED THERMAL GRADIENT

Introduction

Phenotypic plasticity in traits that can directly influence life history parameters is important for organisms that live in variable environments (Caswell 1983, Stearns and Koella 1986). Phenotypic plasticity in life-history traits allows organisms to adapt to a wider range of abiotic factors than could otherwise be tolerated or inhabited with an environmentally-independent (i.e., fixed) phenotype (Via and Lande 1985). For ectotherms, such as turtles, an important abiotic factor that influences phenotypic traits that can directly influence life history parameters is temperature (Laudien 1973, Lillywhite et al. 1973, Gibbons et al. 1981, Bronikowski et al. 2001).

Temperature is important for chelonian physiology and life history characteristics (Bull et al. 1982, Spotila et al. 1984, Rhen and Lang 1995, Mullins and Janzen 2006). Incubation temperature can influence the development rate and sex of turtle embryos (Vogt and Bull 1984) and the growth rate of hatchlings (Rhen and Lang 1995, Roosenburg and Kelley 1996). In hatchling, juvenile, and adult turtles, temperature is positively correlated with metabolism through thermally-induced changes in digestion, ingestion, and assimilation rates (Ellis 1936, Cagle 1946, Gatten 1974, Ernst 1975, Parmenter 1980, Thornhill 1982, Spotila et al. 1984, Brown and Brooks 1991, Frazer et al. 1993, Brown et al. 1994, Cadi and Joly 2003). Increased temperatures leading to increased physiological rates have been implicated in increasing juvenile turtle growth rate (Cagle 1946, Gibbons et al. 1981), leading to increased survivorship, earlier sexual maturation, and larger body size at various stages, including maturation (Bury 1979, Thornhill 1982, Cox et al. 1991, Tucker 2000). Larger body size and earlier sexual maturation of

turtles can lead to reproductive enhancements such as earlier age at reproduction, increased clutch size, and increased size or quality of eggs (Congdon and Gibbons 1983, 1990, 1996; Lovich et al. 1998). Larger body sizes of sexually mature female turtles have been linked to lower mortality rates associated with nesting excursions (Tucker et al. 1999).

Because temperature's effects on growth rate can greatly influence life history characteristics (Cox et al. 1991), it is important to understand how spatial and temporal variation in temperature affects turtle growth rate. Additionally, plasticity in growth rate may have important implications for turtles as global climate change is resulting in overall warming trends (Schlesinger and Jiang 1991, Manabe and Stouffer 1993, Intergovernmental Panel on Climate Change 2007). Field studies investigating spatial differences in growth rate have been largely limited to studies of populations that are geographically distant or inhabiting artificially-warmed ponds (Parmenter 1980, Gibbons et al. 1981, Thornhill 1982, Spotila et al. 1984, Frazer et al. 1993). Studies of variations in growth rates among turtle populations within a river affected by a naturally-induced temperature gradient are not present in peer-reviewed literature. Temporal variation in growth rate has been identified for northern freshwater turtle populations and attributed to global climate change (Frazer et al. 1991, 1993). No investigations of turtle growth rates have been reported for populations in the central United States.

The North Fork of White River (NFWR), Ozark County, Missouri receives a large volume of water from several major springs, which creates a temperature gradient along the stream's length (Nickerson and Mays 1973). NFWR supports a diverse turtle community, predominated by the Northern Map Turtle, *Graptemys geographica* (Pitt 2005). The turtle community within a 4.6 km section of NFWR has been studied periodically since 1969 (Nickerson and Mays 1973, Pitt 2005). Due to the availability of data dating back to 1969 and the natural thermal gradient

created by the spring effluents, NFWR provided a unique opportunity to examine if temporal and spatial differences in growth rates of river turtles occur. My objective was to determine whether instantaneous growth rates of *G. geographica* vary temporally and spatially in a river with a natural thermal gradient.

Materials and Methods

I selected two research sections within the NFWR based on their physical similarities, ease of access, locations relative to the major spring-flows, and suspected difference in mean water temperatures. The first area is the 4.6 km section studied by Nickerson and Mays (1973) and Pitt (2005). This section is located downstream of the major springs and is relatively cool for much of the year, but especially during the summer months. This section was originally surveyed in 1969 with follow-up surveys occurring in 1970, 1971, 1972, 1980 (Nickerson unpublished data), and 2004 (Pitt 2005). The second area is a 4.6 km section located upstream of the major springs and is warmer than the downstream section for much of the year, but especially during the summer months. The two research sections are separated by approximately 16 river kilometers.

I divided each of the two 4.6 km study sections into fifty 92-m-long stations, following the protocol of Nickerson and Mays (1973). In 2005, 2006, and 2007, a research assistant and I surveyed the research sections on alternating days throughout the summer (June 15 – August 20) between 0900 and 1800 h, weather permitting. The downstream section was surveyed for a total of 415 person hours. The upstream section was surveyed for a total of 351 person hours. I recorded air and water temperatures at the beginning of each sampling day. I compared values obtained for each site using independent sample t-tests to determine whether significant differences in air or water temperatures existed between upstream and downstream research sections.

Surveys were conducted by snorkeling paired with mark-recapture techniques. All species of turtles observed in NFWR were indiscriminately captured as this study was part of a broader investigation. However, only techniques and data regarding *G. geographica* will be discussed as the small sample sizes of other species precluded their inclusion in this study. Snorkeling is useful for capturing *G. geographica*, which are difficult to trap. Methods that rely on traps (see Lagler 1943, Chaney and Smith 1950, Braid 1974, Vogt 1980b) are less effective for *G. geographica*, which may not respond to bait (Lagler 1943) and are wary of traps (Pluto and Bellis 1986). Additionally, suggested traps (see Lagler 1943, Chaney and Smith 1950, Vogt 1980b) are time consuming to assemble, cumbersome, and difficult to use in a heavily-trafficked stream like the North Fork (Pluto and Bellis 1986). Hand-capturing methods allowed for behavioral observations of the turtles.

All captured turtles were weighed, measured, and marked using nail polish following the protocol of Pitt (2005). Larger turtles (plastron length ≥ 8.6 cm) were also marked with a passive integrated transponder (PIT) tag (Destron-Fearing Corporation, So. St. Paul, MN, USA) injected into the anterior inguinal region parallel to the bridge of the shell following the protocol of Buhlmann and Tuberville (1998). I disinfected injection sites and needles using 70% isopropyl alcohol and antibiotic ointment. I applied New-Skin Liquid Bandage (Medtech Laboratories, Inc., Jackson, WY, USA) to cover the injection hole. Previous studies from the downstream section of NFWR indicated that both nail polish mark and PIT tag retention were high (Pitt 2005) and appropriate for the purposes of this study. I measured the body temperature of larger *G. geographica* (PL > 5.4 cm) upon capture by inserting a T-6300 Quick-Reading Thermometer (Miller and Weber, Inc., Queens, NY, USA) into the cloaca. The thermometer was inserted a depth of approximately one fifth of the length of the plastron length into the cloaca.

Body temperature was recorded for male and female turtles with plastron lengths greater than 5.6 cm and 6.2 cm, respectively, due to size constraints. I compared body temperatures of *G. geographica*, partitioned by sex, using independent sample t-tests when assumptions of normality and equal variance were met. I conducted nonparametric Mann-Whitney U tests when samples exhibited non-normal distributions and/or unequal variances. I evaluated assumptions of normality and equal variance using the Kolmogorov-Smirnov and Levene analyses, respectively. I visually determined turtles' sex when possible based on morphological characteristics, including relative tail length and thickness. I used chi-squared (χ^2) tests of independence to identify if sex ratios of *G. geographica* differed between sampling sites or periods. I conducted binomial tests to identify if sex ratios differed from 1:1 (male:female).

I calculated individual instantaneous growth rates (ΔGR) using the equation (Cox et al. 1991, Brown et al. 1994):

$$\Delta\text{GR} = (\log_e X_2 - \log_e X_1) / (t_2 - t_1), \quad (3-1)$$

where X_1 and X_2 represent the measurements of the initial and final plastron lengths, respectively, and $t_2 - t_1$ represents the time interval in years that passed between the measuring events. This equation was modified from Brody (1945). Individuals for which sex could be determined must have had a minimum of 30 days between initial capture and recapture events to be included in growth rate analyses. Individuals for which sex could not be determined (i.e., indeterminate sex = hatchlings and post-hatchling juveniles) must have had a minimum of 7 days between initial capture and recapture events to be included in growth rate analyses. Only the final and initial measurements for each turtle were used to ensure that each individual was included only once in the analysis.

I compared instantaneous growth rates observed for *G. geographica* in the downstream section during previous (1969 to 1972) and recent (2004 to 2007) sample years to assess whether changes in growth rate occurred over time. I compared instantaneous growth rates observed for *G. geographica* in recent years (2005 to 2007) in the downstream and upstream sections to assess whether differences in growth rate are apparent in relatively close locations with differing thermal regimes. I evaluated differences in instantaneous growth rates, partitioned by sex, using the nonparametric Mann-Whitney U test as data sets exhibited non-normal distributions and/or unequal variances.

Different time intervals introduce varying degrees of error into the calculation of instantaneous growth rate (Parchevsky 2000). Because the time period between capture events could range from seven days to four years for individuals of indeterminate sex and 30 days to four years for larger juveniles and adults, I investigated if analyses would yield different results if mean time periods were similar or significantly different. When a significant difference in mean time between capture events was detected using either independent sample t-tests or nonparametric Mann-Whitney U tests, as appropriate, I reevaluated sub-samples of the original data sets using a nonparametric Mann-Whitney U test. These sub-samples included only individuals that were captured and recaptured within one sampling season (i.e., less than 3 months).

I documented the behavior of *G. geographica* prior to disturbance and capture. I categorized behavior as either “basking” or “submerged”. “Basking” was used to describe the behavior of any turtle that had emerged onto any substrate that allowed the majority of the turtle’s body to be outside of the water. Typical basking substrates included rocks, fallen trees or branches, emergent vegetation or algal mats, and the riverbank. “Submerged” was used to

describe any behavior of any turtle that maintained the majority of its body in the water. Typical submerged behaviors included swimming, feeding, and bottom-walking. I compared the behavior of *G. geographica*, partitioned by sex, of the 1969 to 1972 and 2004 to 2007 populations within the downstream section using a chi-squared test of independence. I also compared behavior of *G. geographica*, partitioned by sex, of the upstream and downstream populations using a chi-squared test of independence.

I gathered climatological data for south central Missouri for 1969 to 1972 and 2004 to 2007 from the National Oceanic and Atmospheric Administration (NOAA) database. The annual number of degree days and the deviation of monthly temperatures from the normal mean temperatures observed in 1971 to 2000 were compared to assess the relative warmth and growing seasons of given years. Degree days, as included in NOAA datasets were calculated by adding one degree day unit for every degree that the mean daily temperature for that day exceeded 65°F (approximately 18.3 °C) for each day of the year. Koper and Brooks (2000) presented a modification of the degree day heat index which may be more relevant to temperate species of freshwater turtles inhabiting central and northern United States and southern Canada. Koper and Brooks' (2000) heat index was calculated by adding one degree day unit for every degree that the mean daily temperature for that day exceeded 15 °C for each day of the year. Fifteen degrees Celsius was selected as the critical temperature for Koper and Brooks' (2000) calculation because it was the minimum air temperature at which painted turtles, *Chrysemys picta* (Schneider), were observed feeding. Unfortunately, critical temperature data associated with feeding are not available for *G. geographica*. However, the use of 15 °C as an air temperature threshold for feeding may be justified as a rough estimate for *G. geographica*. *Chrysemys picta* and *G. geographica* belong to the same family of turtles, Emydidae (Ernst et al. 1994). The

geographic distribution of *C. picta* almost entirely overlaps that of *G. geographica* (Ernst et al. 1994). In Missouri, *C. picta* and *G. geographica* are active during the same time period (late March – October) (Johnson 2000). In Missouri, the time period of late March through October corresponds with daily temperature means and maximums that equal or exceed 15 °C (National Oceanic and Atmospheric Administration (NOAA) 2004b). Active periods, which include feeding, for turtles are related to temperature (Hutchison 1979, Mahmoud and Klicka 1979) and active periods of *C. picta* and *G. geographica* in Missouri correspond with months when mean and maximum daily temperatures equal or exceed 15 °C. Therefore, I used 15 °C as an estimate for assessing active and growth periods for *G. geographica*. I will refer to Koper and Brooks' (2000) heat index as 'growth days' from this point forward in this manuscript. I used simple linear regression to determine if instantaneous growth rate was correlated with the number of growth days within a year for data sets that yielded significant differences in instantaneous growth rates. I performed statistical analyses using SPSS version 11.5 (SPSS Inc., Chicago, IL, USA) with $\alpha = 0.05$.

Results

Air temperatures were not significantly different between research sections ($t = 0.452$, $df = 72$, $p = 0.653$; Table 3-1). Water temperatures were significantly cooler in the downstream section than in the upstream section ($t = -16.9$, $df = 74$, $p = 0.000$; Table 3-1). Correspondingly, turtle body temperatures observed in the downstream section were significantly cooler than those in the upstream section (females: $t = -3.1$, $df = 51$, $p = 0.003$; males: $z = -4.2$, $p = 0.000$; Table 3-1).

Sex ratios of *G. geographica* for which sex could be visually determined were not significantly different between sampling sites ($\chi^2 = 0.2195$, $df = 1$, $p > 0.05$) or sampling periods

($\chi^2 = 0.2620$, $df = 1$, $p > 0.05$). Sex ratios of *G. geographica* for which sex could be visually determined were not significantly different from a 1:1 (male:female) ratio in either sampling site (Downstream₂₀₀₅₋₂₀₀₇: $p = 1.00$; Upstream₂₀₀₅₋₂₀₀₇: $p = 0.604$) or sampling period (Downstream₁₉₆₉₋₁₉₇₂: $p = 1.00$; Downstream₂₀₀₄₋₂₀₀₇: $p = 0.501$).

Comparison of previous (1969 to 1972) and recent (2004 to 2007) instantaneous growth rates observed in the downstream section indicated that growth rates of males and females were not significantly different between sampling periods (males: $z = -0.578$, $p = 0.563$; females: $z = -0.738$, $p = 0.461$; Table 3-2). No significant differences in mean days between capture events were detected for male or female *G. geographica* between sampling years (males: $z = -1.602$, $p = 0.109$; females: $z = -0.665$, $p = 0.506$; Table 3-2). Individuals too small for sex to be determined based on external diagnostic characteristics (i.e., indeterminate sex) had a significantly greater mean instantaneous growth rate in 2004 to 2007 than in 1969 to 1972 ($z = -3.100$, $p = 0.002$; Table 3-2). A significant difference in days between capture events was observed for *G. geographica* of indeterminate sex ($z = -2.643$, $p = 0.008$; Table 3-2). This variation was due to differences in permanence of marking techniques as carapace notching was not an approved technique by the University of Florida's Institutional Animal Care and Use Committee for recent study years. A subset of the 1969 to 1972 data that included only the individuals for which initial and final capture events occurred in the same sampling season was compared to data from recent years. No significant differences in days between capture events were observed ($t = 1.955$, $df = 15$, $p = 0.069$; Table 3-2). Individuals for which sex could not be determined still had a significantly greater mean instantaneous growth rate in recent years than in 1969 to 1972 ($z = -2.148$, $p = 0.032$; Table 3-2)

No significant differences in instantaneous growth rates of *G. geographica* populations in the downstream and upstream sections were observed (males: $z = -0.919$, $p = 0.363$; females: $z = -1.209$, $p = 0.227$; indeterminate sex: $z = -0.619$, $p = 0.536$; Table 3-3). No significant differences in mean days between capture events were detected (males: $z = -0.991$, $p = 0.322$; females: $z = -0.410$, $p = 0.682$; indeterminate sex: $t = 1.924$, $df = 16$, $p = 0.072$; Table 3-3).

Behavioral differences were not observed between sampling periods for the downstream *G. geographica* population (indeterminate sex: $\chi^2 = 0.3259$, $df = 1$, $p > 0.05$; female: $\chi^2 = 3.1044$, $df = 1$, $p > 0.05$; male: $\chi^2 = 1.2447$, $df = 1$, $p > 0.05$; Table 3-4).

Analyses revealed that behavior of all sexes was dependent on the research section in which the turtles were found (indeterminate sex: $\chi^2 = 7.8466$, $df = 1$, $p < 0.01$; female: $\chi^2 = 28.0507$, $df = 1$, $p < 0.001$; male: $\chi^2 = 22.8975$, $df = 1$, $p < 0.001$; Table 3-5). *Graptemys geographica* inhabiting the downstream research section were observed basking more often than was expected by chance, while those inhabiting the upstream section were more often found submerged (Table 3-5).

There were more degree days and growth days in 2004 to 2007 than in 1969 to 1972 (Table 3-6). Temperatures in March, which mark the beginning of the active season of *G. geographica* in Missouri (Johnson 2000), were warmer in 2004 to 2007 than in 1969 to 1972 (Tables 3-7 and 3-8). March, April, May, August, and October had more growth days in 2004 to 2007 than in 1969 to 1972 (Table 3-7).

Simple linear regression analysis indicated that instantaneous growth rates of individuals in which sex was indeterminate were significantly correlated with the annual number of growth days for the year in which the turtles were first captured (Pearson's correlation = 0.542, $p = 0.005$). Variation in growth days explained 29.4% of variation in instantaneous growth rates (R^2

= 0.294) (Figure 3-1A). Regression analysis yielded similar results for samples in which only individuals that were captured within a single sampling season were included (Pearson's correlation = 0.576, $p = 0.008$; $R^2 = 0.332$; Figure 3-1B).

A major assumption of this research is that the turtle populations compared are distinct (i.e., individuals observed in 1969 to 1972 differ from those observed in 2004 to 2007 and no migration between downstream and upstream populations occurred in 2005 to 2007). *Graptemys geographica* captured in 1969 to 1972 were marked by carapace notching and inspected for notches in 2004 to 2007. No distinct notches were observed, but notches can become obscured with age (Plummer 1979). Ernst et al. (1994) suggest that *G. geographica* may live to at least 20 years of age. If twenty years is an accurate estimate of longevity, it is unlikely that many, if any, turtles captured in 1969 to 1972 would be present in 2004 to 2007, 32 years later.

Based on historical (Nickerson unpublished data, Pitt 2005) and recent (see Chapter 2) *G. geographica* movement estimates within NFWR, the two research sections are distant enough that natural migration between *G. geographica* populations is unlikely. Any natural migration attempted would be limited by a man-made boulder line located between the two sections. The boulder line was placed to create a water retention area adjacent to a resort. If exchange between populations did occur, it would be possible to identify the origin of tagged individuals.

One confounding factor is human-facilitated migration because canoeists will occasionally capture and carry individuals for the length of their float (personal observation). During this three-year study, only one tagged individual from upstream was found in the downstream section. This suggests that though canoeists may occasionally carry turtles downstream, it is either rare that this transportation happens or unlikely that turtles from the upstream section are

deposited in the downstream section. In either scenario, exchange between populations remains extremely low and what does occur is likely unidirectional.

Similarly, unidirectional transport may occur with significant flooding. In 1970, flooding dislodged a large tree from within the downstream research section and deposited it outside of the research section (Nickerson et al. 2007). Despite this disturbance, many turtles were recaptured within the same or proximate areas in which they were originally captured (M. Nickerson personal communication). A flood in July 2007 that was large enough to submerge all but the very tops of the largest boulders (i.e., water rose approximately 1 meter in depth) did not appear to affect the distribution of *G. geographica* within NFWR as recaptures of turtles within their usual capture sites following the flood were common. These data suggest that turtles have behavioral adaptations that counteract, diminish, or eliminate any potential displacement associated with flooding.

Discussion

Temporal variation in climatic temperature regimes has a stronger influence on *G. geographica* growth rate than does spatial variation in the aquatic thermal environment. Differences in growth rate are more detectable among turtles for which sex cannot be determined visually (i.e., indeterminate sex, hatchlings, post-hatchlings).

Graptemys geographica for which sex was visibly indistinguishable (i.e., indeterminate sex) in NFWR in 2004 to 2007 grew approximately 2.8 times faster than similarly-sized turtles in the same section in 1969 to 1972 (Table 3-2). This pattern was significantly correlated with an increased number of growth days in 2004 to 2007 than in 1969 to 1972 (Tables 3-6 and 3-7, Figure 3-1). These results support the hypothesis that climatic variation may affect the growth rate of turtles.

However, growth rate, partitioned by sex, of *G. geographica* for which sex was distinguishable (i.e., older juveniles and adults) was not significantly different between sampling periods (Table 3-2). Growth rate declines as turtles approach sexual maturity and adult turtle growth rates show little variation compared to that of juveniles (Cagle 1946, Chen and Lue 2002). Because of these patterns, differences in growth rates of adults should be minimal. These results should not be interpreted as differences in number of growth days does not affect turtle populations because the enhanced growth rates of smaller turtles may result in higher survival, earlier sexual maturation, or maturation at a larger body size (Bury 1979, Gibbons et al. 1981, Thornhill 1982, Cox et al. 1991, Tucker 2000). Earlier maturation would allow turtles to increase lifetime reproductive output (Gibbons et al. 1981). Similarly, larger body size at maturation is linked to larger clutch size for females and enhanced survival for both sexes (Gibbons et al. 1981, Thornhill 1982, Congdon and Gibbons 1983, Tucker et al. 1999). It is possible that, due to the enhanced growth rates of the juvenile turtles, individuals in 2004 to 2007 may be maturing at an earlier age or larger size than those in 1969 to 1972. Because data for the downstream population in 1969 to 1972 does not include age or size at maturity estimates, comparison of these parameters between sampling periods is impossible.

No significant differences in instantaneous growth rate were observed between the upstream and downstream *G. geographica* populations, partitioned by sex, in 2005 to 2007 (Table 3-3). This pattern is unexpected as differences in water temperature have been implicated as contributors to variation in turtle growth rates (Cagle 1946, Brown et al. 1994, Chen and Lue 2002). Mean water temperature of the upstream section was 5 °C higher than mean water temperature of the downstream section, despite no significant difference in air temperatures (Table 3-1). This result was expected due to distribution of springs along NFWR.

Correspondingly, *G. geographica* body temperatures, partitioned by sex, were significantly higher by approximately 2 °C for turtles captured in the upstream section than in the downstream section. Lower body temperatures among turtles located in a cooler water body are expected because turtle body temperatures are often correlated with water temperatures (Brown et al. 1994). However, turtles were able to maintain their body temperatures on average only 2 °C different when mean water temperatures were 5 °C different. This discrepancy is explained by behavioral differences between the two populations (Table 3-5). *Graptemys geographica* in the upstream section are submerged more often than those in the downstream section (Table 3-5). Therefore, *G. geographica* in the colder portion of the stream (i.e., downstream section) are partially overcoming the thermal regimes of their environments by basking.

Slider turtle (*Trachemys scripta*) populations inhabiting water bodies subjected to thermal effluents of power plants grew faster than those inhabiting similar water bodies with natural thermal regimes (Parmenter 1980, Thornhill 1982). The mean difference in water temperature between the natural and thermally-impacted water bodies in both studies was 5 °C (Parmenter 1980, Thornhill 1982). Both authors suggested that the difference in water temperature accounted, in part, for differences in turtle growth rate (Parmenter 1980, Thornhill 1982). Despite a 5 °C difference in water temperature between the two sections of NFWR, no difference in growth rate was observed. The discrepancy in results between this study and those conducted by Parmenter (1980) and Thornhill (1982) suggest that difference in temperature alone cannot increase turtle growth rate.

Spotilla et al. (1984) determined that turtles in the same thermally-impacted pond studied by Parmenter (1980) did not aerially bask, but turtles in the natural pond were often observed

aerially basking. This behavioral pattern is similar to what I observed in NFWR. Therefore, behavioral patterns are not responsible for the discrepancy in results.

Parmenter (1980) suggested that the difference in food availability and quality in the study ponds he compared were partially responsible for the difference in growth rate. Thornhill (1982) did not find a difference in diet quantity or quality among turtle populations he investigated. These results suggest that diet was not influential enough to create a disparity between the observations of Parmenter (1980) and Thornhill (1982). Therefore, any potential dietary inconsistencies that may exist between the populations in NFWR are probably not responsible for the observed lack of growth rate differences.

Thornhill (1982) suggested that the length of growing season was longer in thermally-impacted ponds and lakes. The longer growing seasons were responsible for the differences in growth rates among populations (Thornhill 1982). In NFWR, the upstream section is significantly warmer throughout the summer months, but because the water temperature varies naturally with air temperature, the length of the growing season of the upstream section will not be enhanced relative to the downstream section. The water in the downstream section may also be buffered by spring effluents so that the temperature is more constant or stable than that of the upstream section. Nickerson and Mays (1973) found that water temperatures in December and January could be upwards of 10 °C in the downstream section. This proposed buffering effect may increase the growing season of the downstream section relative to the upstream section, yielding turtles with similar growth rates.

The hypothesis that the growing season is responsible for differences in turtle growth rates is further supported by the differences in turtle growth rate observed between *G. geographica* in 1969 to 1972 and 2004 to 2007. More growth days and degree days were observed for 2004 to

2007 than 1969 to 1972 (Table 3-6). When monthly growth days are analyzed separately, March, April, May, August, and October all had more growth days in 2004 to 2007 than in 1969 to 1972 (Table 3-7). March and October mark the start and finish of the growing season, respectively (Johnson 2000) and the increased number of growth days in 2004 to 2007 (Table 3-7) suggests that the growing season in recent years was extended. These results are in accord with those found by Frazer et al. (1993) for a population of painted turtles (*Chrysemys picta*) in Michigan.

Conclusions

This study indicates that an extension of the growing season can increase turtle growth rate.

Graptemys geographica growth rate in NFWR did not vary spatially (Table 3-3) despite a significant difference in water temperature created by spring effluents (Table 3-1). *Graptemys geographica* growth rate in NFWR did vary temporally (Table 3-2). Temporal variation was significantly correlated with the number of growth days in the year of capture (Figure 3-1).

Global climate change models predict earlier onset of spring and summer climate patterns (Gates 1993, Intergovernmental Panel on Climate Change 2007). Earlier onset of spring and summer thermal and hydrological regimes is predicted to alter phenology (McCarty 2001), such as the onset of organisms' active and growing seasons. If the observed extension of the growing season observed in this study is associated with global climate change, then global climate change, by extension of the growing season, may be altering the growth rate of freshwater turtles inhabiting temperate climates. Variations in growth rate can lead to size-related alterations in survival and fecundity (i.e., life history traits) that can last throughout a turtle's life (Stearns and Koella 1986, Gibbons et al. 1981). Therefore, global climate change, by extension of the

growing season, may influence not only individual turtle's growth rate and other life history traits, but also population parameters.

Understanding phenotypic plasticity in growth rate is essential for predicting the effects of thermal and climatic variances, such as those predicted by global climate change models, on turtle life history traits and populations. As global climate change is resulting in overall warming trends (Schlesinger and Jiang 1991, Manabe and Stouffer 1993, Intergovernmental Panel on Climate Change 2007), phenotypic plasticity in growth rate and other life history traits will be essential for turtles to adjust to shifting abiotic conditions.

Table 3-1. Temperatures of *Graptemys geographica*, surface water, and air observed in the two research sections of the North Fork of White River, Ozark County, Missouri. N represents the sample size.

	Downstream section			Upstream section		
	N	Mean temperature (°C)	Temperature range (°C)	N	Mean temperature (°C)	Temperature range (°C)
Female <i>G. geographica</i> body temperature	27	24.4	20.6 – 29.1	26	26.2	22.8 – 29.8
Male <i>G. geographica</i> body temperature	45	24.8	19.9 – 29.8	29	26.8	22.9 – 29.4
Water temperature	45	18.7	16.4 – 21.4	31	23.7	21.3 – 27.1
Air temperature	45	29.3	20 – 37	29	28.9	18 – 39

Table 3-2. Instantaneous growth rates of *Graptemys geographica* in the downstream section of North Fork of White River, Ozark County, Missouri for years 1969 – 1972 and 2004 – 2007. N represents the sample size. C.I. denotes the confidence interval.

Indeterminate sex* indicates a sub-sample in which mean days between capture events has been limited to one sampling season.

	N	Mean instantaneous growth rate (95% C.I.)	Instantaneous growth rate range	Mean # of days between capture events	# of Days between capture events range
1969 - 1972					
Indeterminate sex	12	0.225 (0.113 – 0.337)	0.019 – 0.493	253	14 – 1071
Indeterminate sex*	7	0.340 (0.216 – 0.465)	0.150 – 0.493	28	14 – 42
Female	16	0.054 (-0.018 – 0.126)	0 – 0.540	419	33 – 764
Male	25	0.009 (0.005 – 0.014)	0 – 0.041	598	61 – 1572
2004 - 2007					
Indeterminate sex	10	0.594 (0.435 – 0.753)	0.166 – 0.817	18	7 – 28
Female	20	0.013 (-0.002 – 0.028)	0 – 0.133	535	31 – 1104
Male	17	0.033 (0.006 – 0.607)	0 – 0.194	443	31 – 1114

Table 3-3. Instantaneous growth rate of *Graptemys geographica* in the downstream and upstream sections of the North Fork of White River, Ozark County, Missouri for years 2005 – 2007. N represents the sample size.

	N	Mean instantaneous growth rate (95% C.I.)	Instantaneous growth rate range	Mean # of days between capture events	# of Days between capture events range
Downstream section					
Indeterminate sex	9	0.642 (0.508 – 0.775)	0.381 – 0.817	19	7 – 28
Female	13	0.019 (-0.006 – 0.430)	0 – 0.133	403	31 – 742
Male	11	0.049 (0.008 – 0.091)	0 – 0.194	259	31 – 757
Upstream section					
Indeterminate sex	9	0.759 (0.549 – 0.970)	0.391 – 1.41	13	7 – 21
Female	13	0.023 (0.010 – 0.362)	0 – 0.063	456	309 – 756
Male	8	0.019 (-0.002 – 0.040)	0 – 0.073	442	39 – 725

Table 3-4. Behavioral observations of *Graptemys geographica* in the downstream section of the North Fork of White River, Ozark County, Missouri for years 1969 – 1972 and 2004 – 2007. N represents the sample size.

	N	# submerged	# basking
1969 – 1972			
Indeterminate sex	40	9	31
Female	27	10	17
Male	24	10	14
2004 – 2007			
Indeterminate sex	125	23	102
Female	97	20	77
Male	107	32	75

Table 3-5. Behavioral observations of *Graptemys geographica* in the downstream and upstream sections of the North Fork of White River, Ozark County, Missouri for years 2005 – 2007. N represents the sample size.

	N	# submerged	# basking
Downstream section			
Indeterminate sex	84	6	78
Female	70	12	58
Male	88	26	62
Upstream section			
Indeterminate sex	110	24	86
Female	65	40	25
Male	85	56	29

Table 3-6. Degree and growth days for south-central Missouri (National Oceanic and Atmospheric Administration 1969, 1970, 1971, 1972, 2004a, 2005, 2006, 2007). Degree days were calculated by adding one degree day unit for every degree that the mean daily temperature for that day exceeded 65°F (approximately 18.3 °C) for each day of the year. Growth days were calculated by adding one degree day unit for every degree that the mean daily temperature for that day exceeded 15 °C for each day of the year.

1969 – 1972			2004 – 2007		
Year	Degree days	Growth days	Year	Degree days	Growth days
1969	1315	1253.3	2004	1065	1117.2
1970	1305	1252.2	2005	1538	1363.3
1971	1249	1248.3	2006	1243	1195.6
1972	1267	1217.5	2007	1474	1390.3
Total	5136	4971.3	Total	5320	5066.4

Table 3-7. Growth days of months in which *Graptemys geographica* are active in south-central Missouri. Growth days were calculated by adding one degree day unit for every degree that the mean daily temperature for that day exceeded 15 °C for each day of the year.

Year	March	April	May	June	July	August	September	October
1969	0	15.6	125.6	228.1	375.6	273.9	174.7	60.0
1970	0	55.6	152.8	211.1	288.6	299.4	214.2	23.1
1971	6.1	26.4	78.9	288.3	279.2	262.5	221.7	79.2
1972	6.2	45.6	107.8	230.6	274.2	295.6	222.8	36.4
Total	10.3	143.2	465.1	958.1	1217.6	1131.4	833.4	198.7
2004	12.2	31.4	155.8	195.6	270.8	224.7	172.2	51.7
2005	0	27.8	90.0	273.6	320.8	351.9	236.7	51.7
2006	14.2	78.1	116.7	225.8	306.1	321.4	101.7	30.6
2007	41.1	23.9	148.3	229.4	268.6	396.1	199.2	75.8
Total	67.5	161.2	510.8	924.4	1166.3	1294.1	709.8	209.8

Table 3-8. Deviation from normal monthly mean temperature (°F) for south-central Missouri.
 Normal mean temperature is based on the period from 1971 – 2000 (National Oceanic
 and Atmospheric Administration 1969, 1970, 1971, 1972, 2004a, 2005, 2006, 2007).

Year	March	April	May	June	July	August	September	October
1969	-5.8	1.8	2	0.8	3.7	-1	1.6	0.1
1970	-4.4	4	3.6	-0.2	-1.3	0.7	4	-1
1971	-2.1	-0.2	-1.8	4.4	-1.9	-1.7	4	6.2
1972	2	1.8	1.3	0.8	-2.1	0.3	4.1	-1
2004	5.1	1.3	3.2	-1.1	-2.4	-3.8	1.3	2.8
2005	-1.8	1.1	-1.6	3.5	0.5	3.6	5.1	-0.5
2006	1.2	6.3	0.9	0.7	-0.3	1.8	-3.7	-3.3
2007	8.8	-3.0	3.3	0.9	-2.5	6.1	2.8	2.6

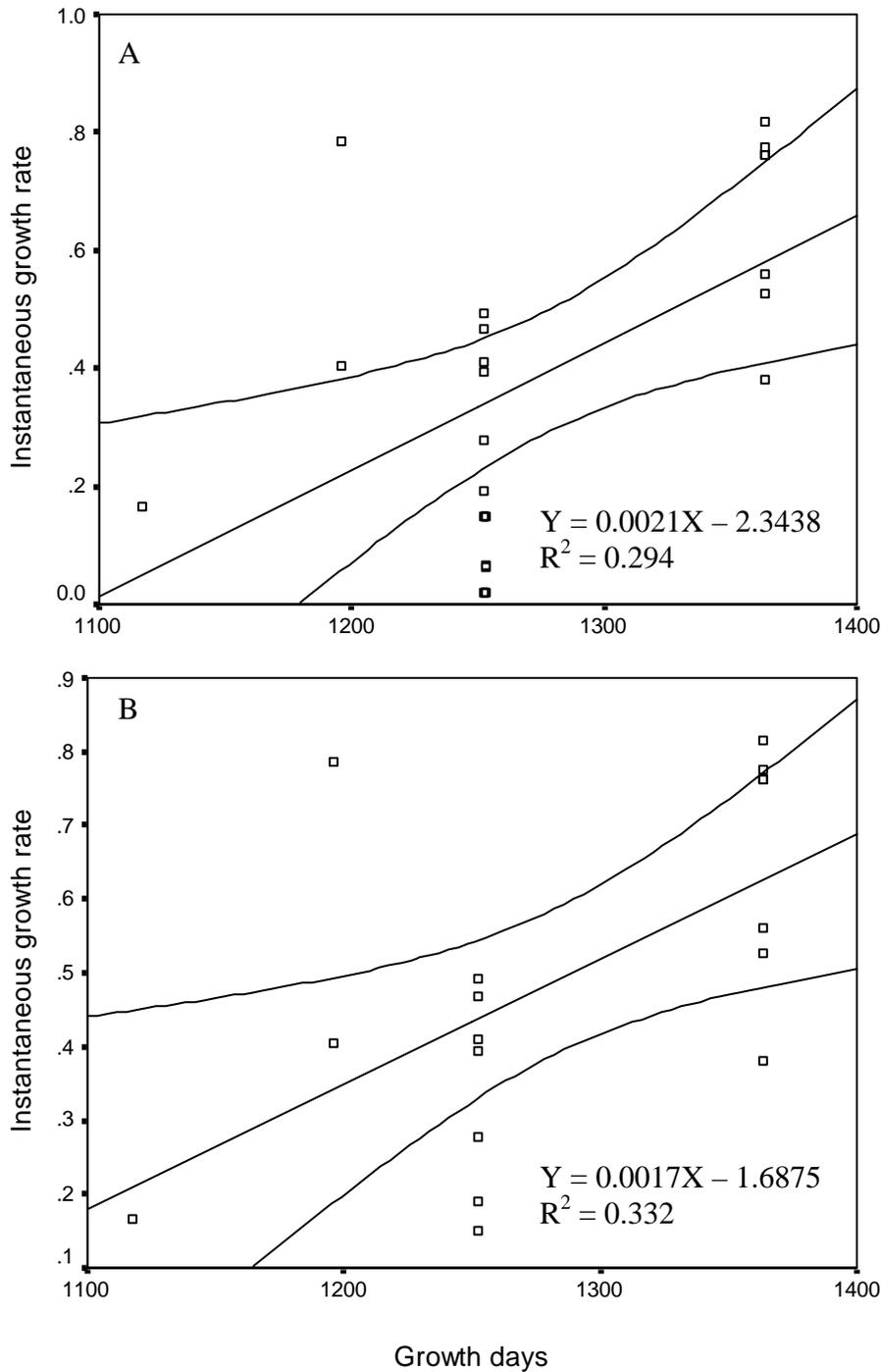


Figure 3-1. Linear regression of individual *Graptemys geographica* instantaneous growth rate and growth days for 1969 – 1972 and 2004 – 2007. (A) *G. geographica* for which sex could not be determined based on visible characteristics. (B) subset of A in which data were restricted to individuals that were captured within the same sampling year. Curved lines represent 95% confidence intervals.

CHAPTER 4
GROWTH CURVE ESTIMATIONS FOR *GRAPTEMYS GEOGRAPHICA* INHABITING THE
NORTH FORK OF WHITE RIVER, OZARK COUNTY, MISSOURI

Introduction

Growth curve estimates obtained by generation of growth models based on field observations can provide estimates of age at sexual maturity and highlight differences in life history characteristics between sexes and among populations and taxa (Frazer et al. 1990a, Lindeman 1997). Growth models provide a statistical approach for estimating age of individuals for which a measurement of interest, such as plastron length (PL), is known (Cox et al. 1991). Growth models characterize the mean growth trend for the population in question (Frazer et al. 1990a). Among freshwater turtle populations, the von Bertalanffy growth model has been determined to be the best descriptor of growth (Lindeman 1999).

Von Bertalanffy growth curves have been generated for half of the 12 recognized *Graptemys* species (Ernst et al. 1994, Jones and Hartfield 1995, Lindeman 1999, Lindeman 2005). Lindeman (1999, 2005) created and compared von Bertalanffy growth curves for *G. ouachitensis* (Cagle), *G. pseudogeographica* (Gray), *G. ernsti* (Lovich and McCoy), *G. caglei* (Haynes and McKown), and *G. versa* (Stejneger). Jones and Hartfield (1995) constructed a von Bertalanffy growth curve for *G. oculifera* (Baur). Despite the prevalence of growth modeling for *Graptemys*, no von Bertalanffy growth curves have been estimated for *G. geographica*, one of the more, if not the most, widespread *Graptemys* species (Ernst et al. 1994).

Gordon and MacCulloch (1980) present growth data of *G. geographica* in Canada by plotting changes in plastral length of turtles of unknown age versus year of capture. Iverson (1988) increased the knowledge of *G. geographica* growth trends by comparing plastral lengths with age for individuals in which ages were known or estimated. Though these studies provide

insight into *G. geographica* growth trends, they are limited in their use for comparison with other populations and taxa and do not provide information related to age at maturity.

My first objective was to determine the mean age at maturity of *G. geographica* inhabiting the North Fork of White River (NFWR), Ozark County, Missouri, in 2005 to 2007 using a statistical method. My second objective was to compare the von Bertalanffy growth model variables obtained for *G. geographica* to variables generated for other species of *Graptemys*.

The *G. geographica* population within a 4.6 km section of NFWR has been studied periodically since 1969 (Nickerson and Mays 1973, Pitt 2005). Subsequent studies occurred in 1970, 1971, 1972, 1980 (Nickerson unpublished data), and 2004 (Pitt 2005). Previous analyses (see Chapter 3) suggested that turtles in the recent years (2005 to 2007) were growing faster than turtles in previous years (1969 to 1972). The difference in growth rate was attributed to an extension of growing season (see Chapter 3). These results suggest the question, are differences in growth rates between sample periods significant enough to yield different growth curves and ages at maturity for *G. geographica* populations inhabiting the same section of NFWR during different time periods? My third objective was to determine if von Bertalanffy growth curves and ages at maturity of *G. geographica* populations inhabiting the same area in different time periods varied.

Materials and Methods

I selected two research sections within the NFWR based on their locations, physical similarities, and ease of access. The first area is the 4.6 km section studied by Nickerson and Mays (1973) and Pitt (2005). This section is located downstream of the major springs and is relatively cool for much of the year, but especially during the summer months. This section was originally surveyed in 1969 with follow-up surveys occurring in 1970, 1971, 1972, 1980 (Nickerson unpublished data), and 2004 (Pitt 2005). The second area is a 4.6 km section located

upstream of the major springs and is relatively warm for much of the year, but especially during the summer months. The two research sections are separated by approximately 16 river kilometers.

I divided each of the two 4.6 km study sections into fifty 92-m-long stations, following the protocol of Nickerson and Mays (1973). In 2005, 2006, and 2007, a research assistant and I surveyed the research sections on alternating days throughout the summer (June 15 to August 20) between 0900 and 1800 h, weather permitting. The downstream section was surveyed for a total of 415 person hours. The upstream section was surveyed for a total of 351 person hours.

Surveys were conducted by snorkeling paired with mark-recapture techniques. All species of turtles observed in NFWR were indiscriminately captured as this study was part of a broader investigation. However, only techniques and data regarding *G. geographica* will be discussed as the small sample sizes of other species precluded their inclusion in this study. Snorkeling is useful for capturing *G. geographica*, which are difficult to trap. Methods that rely on traps (see Braid 1974, Chaney and Smith 1950, Lagler 1943, Vogt 1980b) are less effective for *G. geographica*, which may not respond to bait (Lagler 1943) and are wary of traps (Pluto and Bellis 1986). Additionally, suggested traps (see Chaney and Smith 1950, Lagler 1943, Vogt 1980b) are time consuming to assemble, cumbersome, and difficult to use in a heavily-trafficked stream like the North Fork (Pluto and Bellis 1986).

All captured turtles were weighed, measured, and marked using nail polish following the protocol of Pitt (2005). Larger turtles (plastron length ≥ 8.6 cm) were also marked with a passive integrated transponder (PIT) tag (Destron-Fearing Corporation, So. St. Paul, MN, USA) injected into the anterior inguinal region parallel to the bridge of the shell following the protocol of Buhlmann and Tuberville (1998). I disinfected injection sites and needles using 70%

isopropyl alcohol and antibiotic ointment. I applied New-Skin Liquid Bandage (Medtech Laboratories, Inc., Jackson, WY, USA) to cover the injection hole. Previous studies from the downstream section of NFWR indicated that both nail polish mark and PIT tag retention were high (Pitt 2005) and thus appropriate for the purposes of this study. I estimated the age of turtles when possible by counting the annuli on the abdominal lamina. Due to the erosion of annuli with age (Graham 1979), estimates were only possible for very small (i.e., young) turtles. I visually determined turtles' sex when possible based on morphological characteristics, including relative tail length and thickness. I recorded tail length, which is the most apparent and easily measured diagnostic characteristic useful for determining sex in *G. geographica*, for each turtle. I plotted tail length against plastron length to illustrate differences in the relationship of these parameters between sexes. I then calculated the ratio of tail length to plastron length. I plotted plastron length against this ratio to elucidate at what plastron length and ratio of tail length to plastron length differences among sexes become visible.

I calculated individual instantaneous growth rates (ΔGR) using the equation (Brown et al. 1994, Cox et al. 1991):

$$\Delta GR = (\log_e X_2 - \log_e X_1) / (t_2 - t_1) \quad (4-1)$$

where X_1 and X_2 represent the measurements of the initial and final plastron lengths, respectively, and $t_2 - t_1$ represents the time interval in years that passed between the measuring events. This equation was modified from Brody (1945). Individuals for which sex could be determined must have had a minimum of 30 days between initial capture and recapture events to be included in growth rate analyses. Individuals for which sex could not be determined (i.e., indeterminate sex = hatchlings and post-hatchling juveniles) must have had a minimum of seven days between initial capture and recapture events to be included in growth rate analyses. Only

the final and initial measurements for each turtle were used to ensure that each individual was included only once in the analysis.

I evaluated differences in instantaneous growth rates of turtles in the two research sections in 2005 to 2007, partitioned by sex, using the nonparametric Mann-Whitney U test as samples exhibited non-normal distributions and/or unequal variances. I evaluated normality and equal variance using the Kolmogorov-Smirnov and Levene analyses, respectively. Because no significant difference in instantaneous growth rate was observed, I pooled data from the two *G. geographica* populations obtained from the two research sections to create a larger sample size for analysis. I plotted instantaneous growth rates against median plastron length to elucidate the general growth patterns observed for *G. geographica* in NFWR. Median plastron length indicates the median size of a turtle calculated from the plastron length measurements from the initial and final captures.

I compared instantaneous growth rates of male and female *G. geographica* located in NFWR in 2005 to 2007 using a nonparametric Mann-Whitney U test to determine if differences in growth rate of large juvenile and adult turtles could be discerned. A nonparametric test was conducted as data sets had non-normal distributions and/or unequal variances as determined by the Kolmogorov-Smirnov and Levene analyses, respectively.

I compared instantaneous growth rates observed for *G. geographica* in the downstream section during previous (1969 to 1972) sample years with instantaneous growth rates observed for *G. geographica* in the upstream and downstream sections, combined, during recent (2005 to 2007) sample years. I conducted this analysis to assess whether changes in growth rate occurred over time when estimates from recent years from both sections were combined. I evaluated

differences in instantaneous growth rates, partitioned by sex, using the nonparametric Mann-Whitney U test as samples had non-normal distributions and/or unequal variances.

I used recapture data to estimate von Bertalanffy growth curves using the Fabens' method, which accommodates for the lack of age data (Frazer et al. 1990a). Age is difficult to discern in all but the youngest of *G. geographica* because annuli, the typical characteristic used to determine age of turtles, fade with age (Graham 1979, Lindeman 1999). The general von Bertalanffy equation is:

$$L_t = a(1 - be^{-kt}), \quad (4-2)$$

where L_t represents the length at age t , a is the asymptotic length, b is a variable related to the size at hatching, e is Euler's constant (i.e., the base of the natural logarithm), k represents the intrinsic growth rate variable, and t is the age (Frazer et al. 1990a). The Fabens' method allowed for the estimation of growth curves when age was unknown by providing the following rearrangement of the von Bertalanffy equation (Frazer et al. 1990a):

$$L_r = a - (a - L_c)e^{-kd}, \quad (4-3)$$

where L_r and L_c represent the lengths at recapture and initial capture, respectively, and d is the time interval between L_r and L_c . Variables a , e , and k are the same as those found in Equation 4-2.

I estimated variables a and k by fitting mark-recapture data to Equation 4-3 using a non-linear regression analysis conducted with SPSS version 11.5 (SPSS Inc., Chicago, IL, USA). I conducted analyses for each sex with individuals of indeterminate sex (i.e., hatchlings; posthatchlings) included in datasets for both sexes to provide data for the smallest size classes. By solving Equation 4-2 for age zero, a simplified equation is generated as follows:

$$L_0 = a(1 - b), \quad (4-4)$$

and can be rearranged to estimate the value of variable b:

$$b = 1 - (L_0/a) \quad (4-5)$$

(Frazer et al. 1990a). I estimated L_0 , the size at hatching, as the size of the smallest individuals observed (plastron length = 2.4, N = 2). I selected this value for L_0 because all turtles were collected from their aquatic habitat so some indeterminate time had passed since hatching. Because growth occurs rapidly in hatchlings, it was likely that growth had occurred in many of the immature turtles observed. My decision to use the minimum values observed is supported by evidence collected by D. Moll (personal communication). D. Moll (personal communication) found a mean PL of 2.3 cm from 36 *G. geographica* hatchlings (range = 1.9 cm – 3.1 cm) from the Niangua River, Dallas County, Missouri incubated in a laboratory.

I inserted values obtained for a, k, and b into Equation 4-2 and solved for the length at age t for each year of age. I estimated data sets for both sexes individually as *G. geographica* are sexually dimorphic in size and have differing growth curves (Iverson 1988). I plotted data for turtles which had estimated known ages based on annuli counts along with von Bertalanffy growth curves to assess the relative fit of the model estimates. I also estimated a data set for the male *G. geographica* population located in the downstream section of NFWR in 1969 to 1972. Small sample size precluded the generation of a data set for female *G. geographica* present in the same population.

A major assumption of this research is that the von Bertalanffy growth model is representative of the underlying growth function of *Graptemys geographica* in NFWR. The von Bertalanffy growth model has been evaluated in comparison with other models for a diversity of turtle species with mixed results (Chen and Lue 2002, Cox et al. 1991, Iverson et al. 1991, Jones and Hartfield 1995, Lindeman 1997, Lindeman 1999). Lindeman (1997) reviewed the

effectiveness of the von Bertalanffy model for describing freshwater turtle growth and found that it was the most accurate descriptor. Additionally, Lindeman (1999, 2005) and Jones and Hartfield (1995) found that the von Bertalanffy growth model was appropriate for members of the genus *Graptemys*.

Frazer et al. (1990a) demonstrated that Fabens' method was accurate for constructing growth curves of unknown-age individuals of turtles when the von Bertalanffy model represents the underlying growth function.

Results

Relative tail length differences between sexes become apparent as plastron lengths reach approximately 5 cm and tail length to plastron length ratio equals approximately 0.45 (Figures 4-1 and 4-2). Following achievement of plastron lengths of 5 cm, the tail length of males exceeds that of females with corresponding plastron lengths (Figure 4-1).

No significant differences in instantaneous growth rates of *G. geographica* populations in the downstream and upstream sections were observed (males: mean $\Delta\text{GR}_{\text{downstream}} = 0.049$, $\Delta\text{GR}_{\text{upstream}} = 0.019$, $z = -0.919$, $p = 0.363$; females: mean $\Delta\text{GR}_{\text{downstream}} = 0.019$, $\Delta\text{GR}_{\text{upstream}} = 0.023$, $z = -1.209$, $p = 0.227$; indeterminate sex: mean $\Delta\text{GR}_{\text{downstream}} = 0.642$, $\Delta\text{GR}_{\text{upstream}} = 0.759$, $z = -0.619$, $p = 0.536$). Plotting instantaneous growth rate versus median plastron length revealed that the growth rate of *G. geographica* decreases with size and is close or equal to zero at larger sizes (Figure 4-3).

No significant difference in instantaneous growth rate was observed between male and female *G. geographica* inhabiting NFWR in 2005 – 2007 (mean_{male} $\Delta\text{GR} = 0.0368$, mean_{female} $\Delta\text{GR} = 0.0208$, $z = -1.164$, $p = 0.245$).

Comparison of instantaneous growth rates observed in the downstream section in 1969 to 1972 with values for the combined upstream and downstream populations in 2005 to 2007 indicated that growth rates of males and females were not significantly different between sampling years (males: mean $\Delta GR_{1969-1972} = 0.0095$, $\Delta GR_{2005-2007} = 0.0626$, $z = -1.607$, $p = 0.108$; females: mean $\Delta GR_{1969-1972} = 0.0539$, $\Delta GR_{2005-2007} = 0.0208$, $z = -0.222$, $p = 0.825$). Individuals too small for sex to be determined based on external diagnostic characteristics (i.e., indeterminate sex) had a significantly greater mean instantaneous growth rate in 2005 to 2007 than in 1969 to 1972 (mean $\Delta GR_{1969-1972} = 0.2250$, $\Delta GR_{2005-2007} = 0.7335$, $z = -4.061$, $p = 0.000$).

Estimates of variables a and k produced by the nonlinear regression for Equation 4-3 are presented in Table 4-1. Variable b was estimated as 0.714 and 0.879 for male and female *G. geographica* in NFWR in 2005 to 2007, respectively. Variable b was estimated as 0.717 for male *G. geographica* in NFWR in 1969 to 1972. Table 4-2 summarizes von Bertalanffy variable estimates generated in this study with those generated for other members of the genus *Graptemys* by Jones and Hartfield (1995) and Lindeman (1999, 2005).

Based on the growth curves generated for populations in NFWR in 2005 to 2007 (Figure 4-4), male and female *G. geographica* grow at approximately the same rate through their first year. Following the first year, females continue to grow at a high rate while male growth rate slows (Figure 4-4). Females achieve substantially larger body sizes than males (Table 4-1, Figure 4-4). Using Gordon and MacCulloch's (1980) estimates of plastron length at sexual maturity, females in this population mature between 11 and 12 years of age while males mature between three and four years of age.

Comparison of age-estimated turtles' relative size and age-size values obtained from the von Bertalanffy growth models (Figure 4-5) revealed that the von Bertalanffy models were fairly

representative of *G. geographica* growth in NFWR assuming age estimates of turtles captured in the field were reasonably accurate.

Comparison of the von Bertalanffy growth curves calculated for males in 1969 to 1972 and 2005 to 2007 revealed that male *G. geographica* in recent years were growing faster than those observed in previous years (Figure 4-6). Based on Gordon and MacCulloch's (1980) estimate of plastron length at sexual maturity, males in 1969 to 1972 were maturing between seven and eight years of age.

Discussion

Graptemys geographica grow rapidly as hatchlings and juveniles but growth rate declines as turtles attain sexual maturity (Figures 4-3 and 4-4). Male and female *G. geographica* grow at different rates following their first year, with females growing faster and attaining larger body sizes than males (Figure 4-4). These results are in accord with those found by Iverson (1988) for a *G. geographica* population in Indiana. It should be noted that Iverson (1988) stated the growth rates of male and female *G. geographica* in an Indiana population diverged at approximately two years of age, but the trend-lines fitted to the growth data in his study (see Figure 1 in Iverson 1988) suggested that the deviation occurred following one year of age.

At one year of age, *G. geographica* in NFWR had a mean plastron length of 5 cm (Figure 4-4). This was the same size at which the relative tail length became longer for male *G. geographica* (Figures 4-1 and 4-2). This change in growth rate of males in correlation with enhanced tail length relative to females, suggest that a portion of the energy available for growth in males is diverted to the attainment of secondary sexual characteristics, such as increased tail length.

Growth rate decreased sharply for males and females at approximately three to four and 11 to 12 years old, respectively (Figure 4-4). These declines in growth rate likely correspond with

ages at sexual maturity. This hypothesis is supported by estimates of age at maturity generated using plastron lengths at sexual maturity reported by Gordon and MacCulloch (1980). Based on Gordon and MacCulloch's (1980) estimates of plastron lengths at sexual maturity, females in this population mature between 11 and 12 years of age while males mature between three and four years of age. These values are in accord with those found in other studies (Iverson 1988, Vogt 1980a). Iverson (1988) estimated age at maturity for female and male *G. geographica* in Indiana at nine to 10 and three to five years, respectively. Vogt (1980a) estimated that males became sexually mature at four years of age and females after 10 to 12 years of age in a *G. geographica* population in Wisconsin.

Values for asymptotic plastron length (variable a) were just above the mean adult size plastron lengths observed in the NFWR *G. geographica* population (mean $PL_{\text{male}} = 8.4$ cm; mean $PL_{\text{female}} = 19.9$ cm; Table 4-1). According to Frazer et al. (1990a), the generated von Bertalanffy growth curve is a sufficient representation of the actual growth pattern if the mean adult size observed lies just below the estimated values of asymptotic plastron length.

Estimated age-at-size based on annuli counts corresponded with the von Bertalanffy growth curves, but agreement of count data and growth curves was greater for juveniles and males than for females (Figure 4-5). I suspect that age estimates based on annuli counts in this study may be somewhat low for the largest (i.e., older) females in which annuli were still visible. Alternatively, the von Bertalanffy growth curve for female *G. geographica* could be skewed towards a larger size at age. This hypothesis seems unlikely as a reduction in size at age would represent a much slower juvenile growth rate and sexual maturation would be significantly delayed.

Despite the variation in growth rate between sexes as depicted by the von Bertalanffy growth curves, no significant differences in instantaneous growth rates were observed for male and female *G. geographica*. These results suggest that differences in growth rate between sexes are largely attributed to variation in growth rate among juvenile *G. geographica*. The comparisons of instantaneous growth rate data between sexes are incorporating all individuals for which sex was distinguishable. As adult turtle growth rate approaches zero, any differences in growth rate between sexes will be dampened by these near-zero and zero values. If a large enough sample size were available to partition sexes into smaller size classes based on plastron length, I predict that a significant difference in instantaneous growth rates would be observed between smaller and younger male and female *G. geographica*.

Von Bertalanffy parameters estimated in this study for *G. geographica* (Table 4-1) are comparable to those found for other *Graptemys* species of similar size (Table 4-2). These results are expected due to the close phylogenetic relationship of these species.

The von Bertalanffy growth curve estimated for male *G. geographica* inhabiting NFWR in 1969 to 1972 approached asymptotic size at a slower rate than for males in 2005 to 2007 (Figure 4-6). This difference in growth rate is apparent when the intrinsic growth rates (k) of the two populations are examined (Table 4-1). A lower intrinsic growth rate (k) corresponds with a slower approach to asymptotic size (a) (Lindeman 1999). These data suggest that males in 1969 to 1972 matured at seven to eight years of age, twice the age of male *G. geographica* in NFWR in 2005 to 2007. Gibbons et al. (1981) discovered that male slider turtles (*Trachemys scripta*) were maturing at a younger age in a pond receiving thermal effluents from a nuclear power plant. Growth curves presented by Gibbons et al. (1981), suggest that male *T. scripta* were also maturing at a slightly larger size (approximately 1.5 cm larger) in the impacted pond than did

those in the natural pond (see Figure 2 in Gibbons et al. 1981). If a similar size discrepancy of 1.5 cm were observed for *G. geographica* inhabiting NFWR, male *G. geographica* would mature at approximately three to four years in 1969 to 1972, the same age at maturity of those in 2005 to 2007. Mature male *G. geographica* in 1969 to 1972 would have been smaller than those present in 2005 to 2007 (Figure 4-6). In either scenario, male *G. geographica* in NFWR in recent years (2005 to 2007) would benefit from earlier age at maturity or larger size-at-age as their lifetime reproductive output and/or age-specific survival rates should be enhanced. These results suggest that males in recent years are benefiting from an extension of growing season in terms of age at sexual maturity and/or size-at-age enhancements.

Conclusions

This study revealed patterns in growth rate between sexes that account for the extreme sexual size dimorphism observed in *G. geographica*.

Juvenile *G. geographica* grow at a much faster rate than adults (Figures 4-3 and 4-4). A secondary sexual characteristic, relative tail length, becomes apparent when plastron lengths reach 5 cm (Figure 4-1), which corresponds with approximately one year of age (Figure 4-4). Divergence in growth rates between male and female juveniles occurs after one year of age and male *G. geographica* mature at approximately three to four years of age (Figure 4-4). Female *G. geographica* have higher growth rates than males and attain much larger body sizes (Table 4-1, Figure 4-4).

This study provides evidence that an extension of the growing season can reduce the age of maturity of *G. geographica*.

Comparison of von Bertalanffy growth curves indicated that male *G. geographica* were growing more slowly in 1969 to 1972 than those in 2005 to 2007 (Table 4-1, Figure 4-6). The reduction in growth rate corresponds with an estimated older age at maturity of male *G.*

geographica in 1969 to 1972 relative to those in 2005 to 2007 (Figure 4-6). Additionally, for ages less than 16 years, male *G. geographica* in 1969 to 1972 are predicted to be smaller than those in 2005 to 2007 (Figure 4-6). Younger age at maturity is predicted to lead to increased lifetime reproductive output (Gibbons et al. 1981). Additionally, turtles with larger body sizes at any given age are expected to have a greater chance of survival (Gibbons et al. 1981, Janzen 1993, Bodie and Semlitsch 2000, Janzen et al. 2000, Tucker 2000).

This study increases the breadth of knowledge regarding the genera *Graptemys* and the depth of knowledge specific to *G. geographica*. It also provides insight into potential changes in life history characteristics that may occur with global climate change as global climate change is predicted to increase temperatures and result in earlier onset of spring and summer thermal and hydrological regimes (Gates 1993, Intergovernmental Panel on Climate Change 2007). This knowledge will be useful for predicting how populations of *G. geographica*, and perhaps other temperate freshwater turtle species, will adjust to a rapidly changing climate or climatic variation.

Table 4-1. Von Bertalanffy growth curve model variables for *Graptemys geographica* estimated using nonlinear regression techniques.

Sex	Asymptotic length (a) (cm) (95% confidence interval)	Intrinsic growth rate (k) (95% confidence interval)	R ²
1969 - 1972			
Male	8.5 (7.8 – 9.1)	0.2548 (0.1618 – 0.3477)	0.939
2005 - 2007			
Male	8.4 (8.1 – 8.8)	0.5062 (0.2449 – 0.7676)	0.981
Female	19.9 (18.7 – 21.1)	0.1674 (0.1326 – 0.2022)	0.997

Table 4-2. Summary of von Bertalanffy growth curve model variables available for *Graptemys* species. PL represents plastron length. C.I. denotes confidence interval.

Species/sex	Intrinsic growth rate (k) (95% C.I.)	Variable b (95% C.I.)	Asymptotic PL (a) (cm) (95% C.I.)	Data source
<i>G. geographica</i>				
Male	0.506 (0.2449-0.7676)	0.717	8.4 (8.1–8.8)	This study
Female	0.167 (0.1326-0.2022)	0.864	19.9 (18.7-21.1)	This study
<i>G. oculifera</i>				
Male	0.388 (0.3155-0.4613)	0.578	7.82	Jones and Hartfield 1995
Female	0.176 (0.1262-0.2258)	0.754	13.41	Jones and Hartfield 1995
<i>G. versa</i>				
Male	No data	No data	No data	Lindeman 2005
Female	0.194 (0.017-0.371)	0.862 (0.622-1.102)	15.25	Lindeman 2005
<i>G. caglei</i>				
Male	0.445 (0.397-0.493)	0.631 (0.607-0.656)	9.15	Lindeman 1999
Female	No data	No data	16.70	Lindeman 1999
<i>G. ouachitensis</i>				
Male	0.459 (0.417-0.500)	0.740 (0.719-0.761)	9.63	Lindeman 1999
Female	0.182 (0.169-0.194)	0.854 (0.841-0.866)	17.53	Lindeman 1999
<i>G. pseudogeographica</i>				
Male	0.498 (0.438-0.559)	0.779 (0.753-0.805)	11.45	Lindeman 1999
Female	0.161 (0.149-0.174)	0.860 (0.849-0.872)	21.07	Lindeman 1999
<i>G. ernsti</i>				
Male	0.264 (0.248-0.279)	0.672 (0.662-0.681)	9.87	Lindeman 1999
Female	0.110 (0.104-0.116)	0.866 (0.857-0.875)	22.02	Lindeman 1999

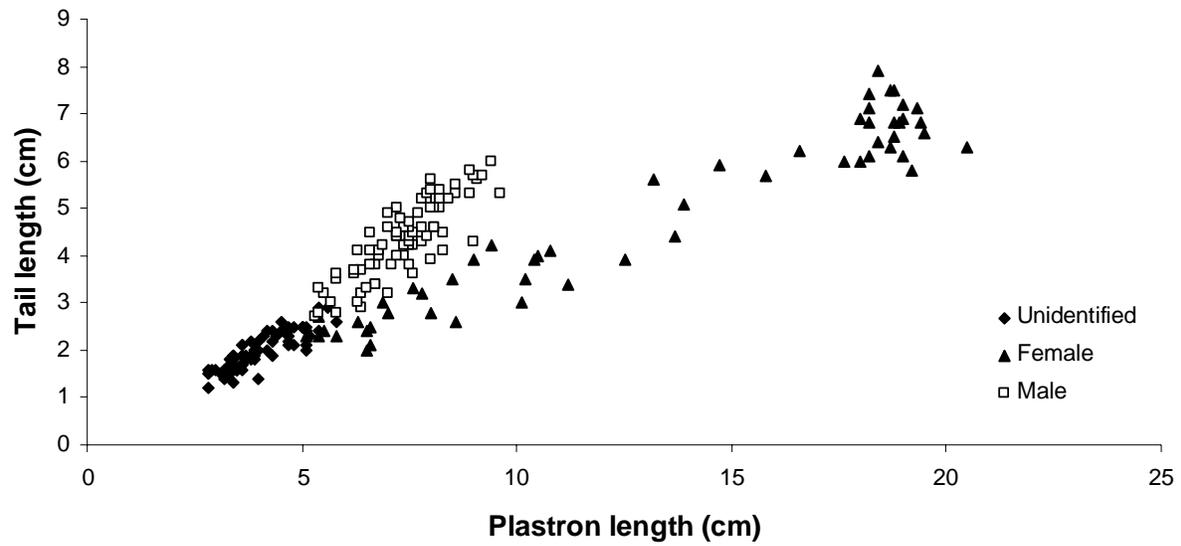


Figure 4-1. Relationship between tail length and plastron length observed in the *Graptemys geographica* population in the North Fork of White River, Ozark County, Missouri for the sampling period 2005 – 2007.

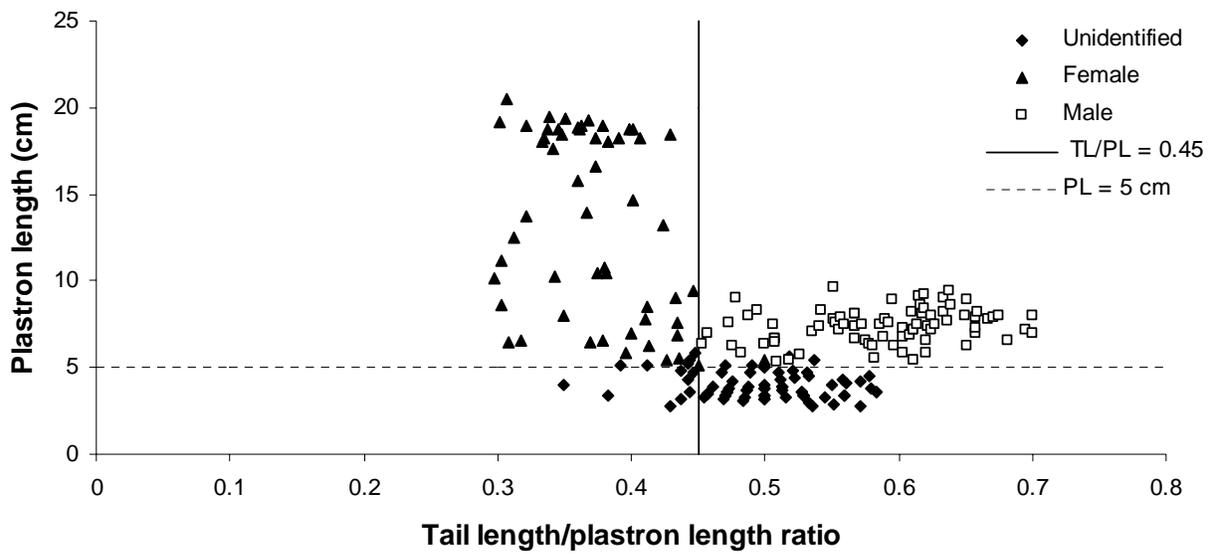


Figure 4-2. Relationship between plastron length and tail length/plastron length ratio observed in the *Graptemys geographica* population in the North Fork of White River, Ozark County, Missouri for the sampling period 2005 – 2007.

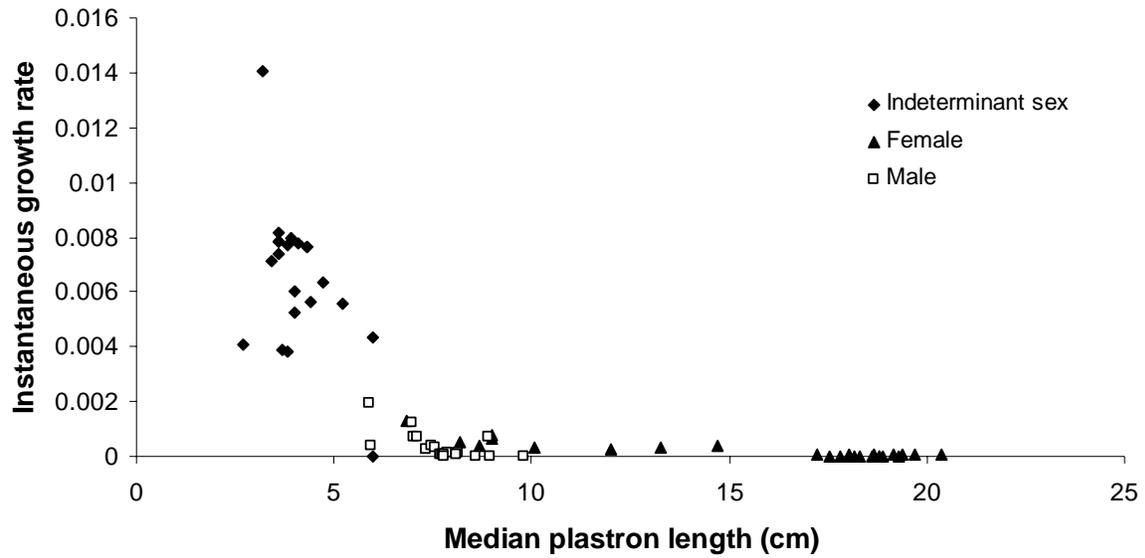


Figure 4-3. General growth pattern observed in the *Graptemys geographica* population in the North Fork of White River, Ozark County, Missouri for the sampling period 2005 – 2007. Median plastron length indicates the median size of a turtle based on the plastron length measurements from the initial and final capture.

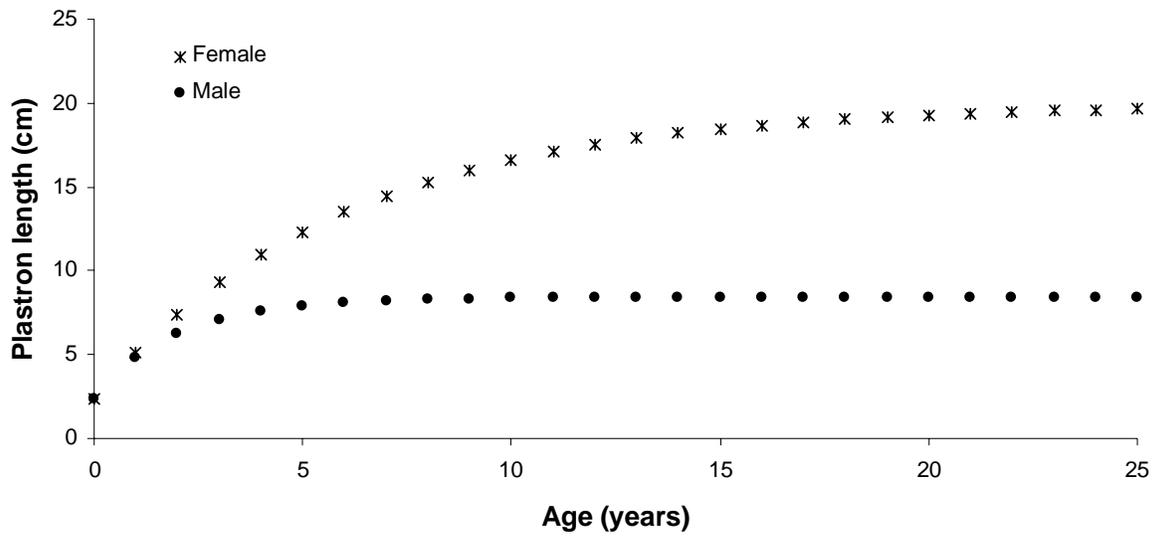


Figure 4-4. Von Bertalanffy growth curves for the *Graptemys geographica* population in the North Fork of White River, Ozark County, Missouri for the sampling period 2005 – 2007.

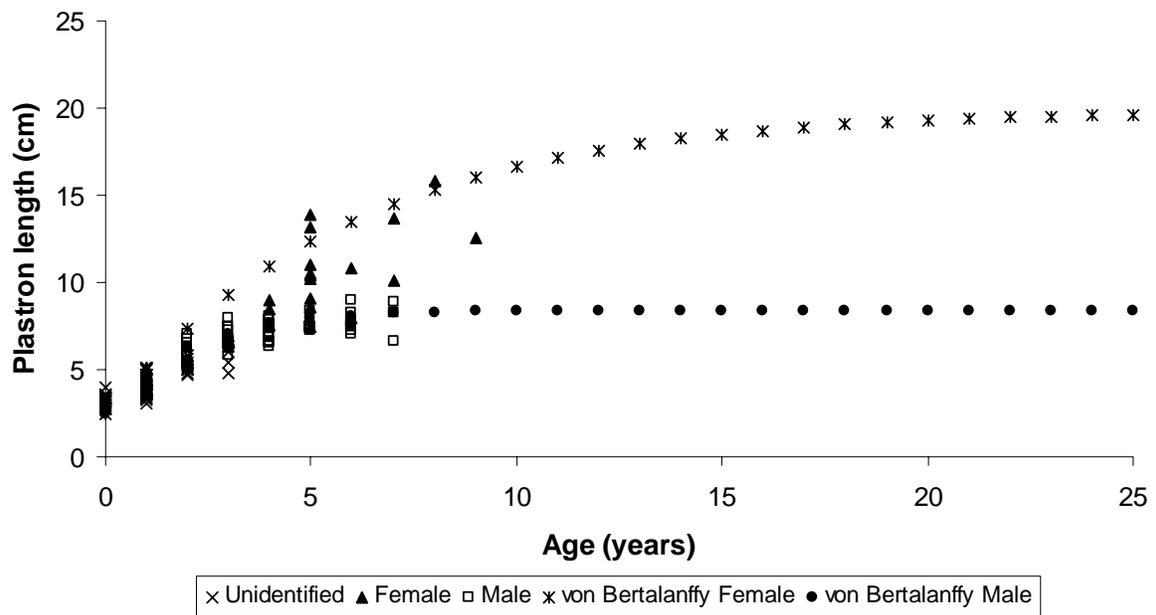


Figure 4-5. Von Bertalanffy growth curves and estimated-age data for *Graptemys geographica* inhabiting the North Fork of White River, Ozark County, Missouri for the sampling period 2005 – 2007.

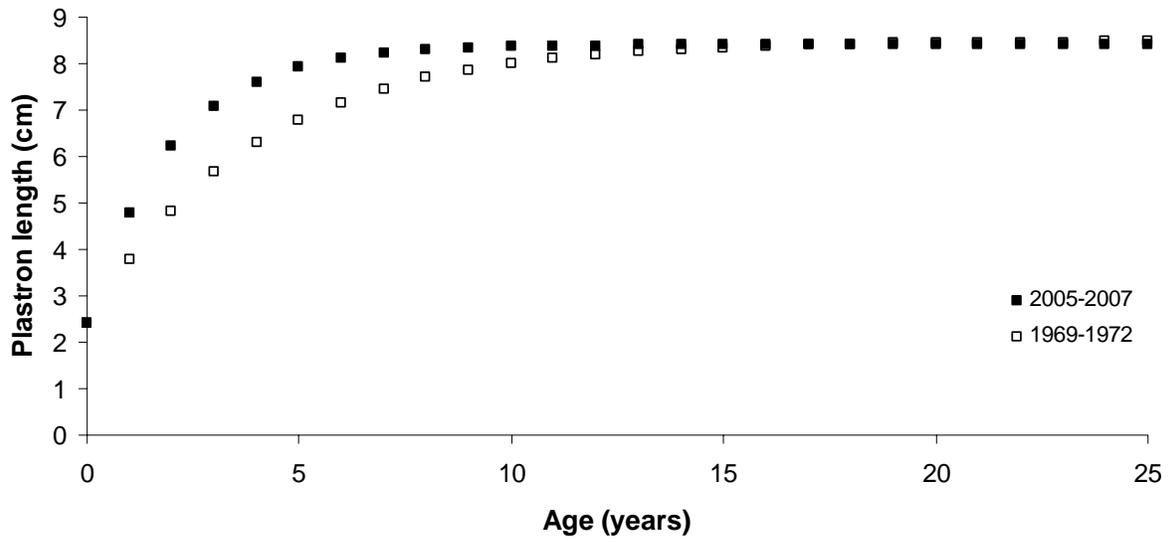


Figure 4-6. Von Bertalanffy growth curves for male *Graptemys geographica* inhabiting the North Fork of White River, Ozark County, Missouri for the sampling periods 1969 – 1972 and 2005 – 2007.

CHAPTER 5 CONCLUSIONS AND RECOMMENDATIONS

In this chapter, I integrated information presented in previous chapters to draw conclusions and make recommendations applicable to future studies both within and outside of NFWR.

Conclusions

Temporal and Spatial Variation in Abiotic Factors Influences River Turtle Community Composition, Species Richness, and Heterogeneity

Nonequilibrium community theories integrate the idea that a perpetually-changing environment (i.e., abiotic factors) can be a major determining force influencing community composition (Chesson and Case 1986). A continually-shifting and heterogeneous environment can cause populations and communities to vary temporally and spatially (Davis 1986, Cody 1996). These ideas are in contrast to classical competition theory which suggests competitive interactions primarily shape communities (Chesson and Case 1986).

Analyses of temporally and spatially- distinct turtle communities and *G. geographica* populations in NFWR support nonequilibrium community theories that suggest variation in abiotic conditions can drive community composition. In Chapter 2, I elucidated a temporal shift in composition of a turtle community located within a 4.6 km section of NFWR that had been studied periodically since 1969. The turtle community shifted from an assemblage of one common species and several rare species to a grouping of several common species and a few rare species (Figure 2-3A). Analysis of species richness suggested the turtle community in 1969 typically had more species than the community inhabiting the same section in recent years (2005, 2006, and 2007) (Figure 2-4A). Comparisons of heterogeneity measures indicated that the turtle community was more heterogeneous in 2005, 2006, and 2007 than was the turtle community in the same section in 1969 (Table 2-1). These results were indicative of the increased species

evenness associated with an increase in *S. odoratus* and *T. s. elegans* observed in the downstream section in 2005, 2006, and 2007 (Figure 2-3A).

The observed community changes corresponded with changes in the abiotic environment. Riparian zone development, degradation of water quality, siltation, and sedimentation occurred between 1969 and recent years (Figures 2-1 and 2-2; Pitt 2005). Development of riparian zones is associated with increased siltation, sedimentation, sun exposure, and bacteria and nutrient-loading (Gilliam 1994, Pusey and Arthington 2003). These factors create ideal conditions for aquatic vegetation growth and algal blooms (Smith et al. 1999, Groom and Vynne 2006), such as that observed in recent years in NFWR. Analysis of basking substrate use indicated that *T. s. elegans* and *S. odoratus* basked overwhelmingly on vegetation in recent years (Table 2-2). *Trachemys scripta elegans* is a highly-adaptable, generalist species that will exploit most habitats (Webb 1961, Vogt and Benitez 1997). The establishment of aquatic vegetation stands and the presence of long-lived, extensive algal blooms provide ample amounts of basking habitat that *T. s. elegans* are able to exploit. Similarly, the increase in abundance of the *S. odoratus* population in NFWR in 2005 corresponded with the growth of emergent vegetation stands and associated algal mats. All but four of the 130 *S. odoratus* observed basking were associated with vegetation (Table 2-2). These emergent vegetation stands were associated with muddy, silty substrates, a typical habitat of *S. odoratus* (Kingsbury 1993). Prior to the establishment of extensive emergent vegetation stands, few *S. odoratus* were observed in NFWR (Pitt 2005), but *S. odoratus* comprised a major portion of the turtle community in 2005 to 2007 (Figure 2-3A). Therefore, I conclude that abiotic changes, including siltation and sedimentation, resulted in substantial vegetation growth and subsequent temporal shifts in turtle populations and communities in NFWR.

Spatial variation among communities was detected when the above described turtle communities, which are located in a 4.6 km section located downstream of major spring flows entering NFWR, were compared with the turtle communities inhabiting a 4.6 km section of NFWR located upstream of the major spring flows. The community in the downstream section typically had lower species richness, indicating fewer species, than the turtle community in upstream section in recent years (Figures 2-4C, D, and F). The turtle community in the downstream section was more heterogeneous than the upstream turtle community in recent years (Table 2-1). These results indicate that the upstream section contained more rare turtle species than the downstream section in 2005 to 2007.

Differences in turtle communities inhabiting the two sections corresponded with differences in habitat. Water temperature was warmer in the upstream section than in the downstream section. More species are expected to inhabit areas with warmer water as turtles tend to move to and among areas of favorable thermal regimes (Schuett and Gatten 1980, Thornhill 1982, Moll and Moll 2004) and the distribution of some species may be limited by temperature. The upstream section exhibited fewer symptoms of human impact than did the downstream section. Riparian zone development was less prevalent in the upstream section than in the downstream section. The upstream section had fewer stations that tested positive for excessive *E. coli* levels (Figure 2-2). The upstream section had less aquatic vegetation, indicating less nutrient-loading. If turtles prefer less-impacted habitats, more species would be expected in the less-impacted habitat.

The community composition, species richness, and heterogeneity of the turtle communities located in the upstream section in 2005 to 2007 and in the downstream section in 1969 were relatively similar (Figures 2-3 A and 2-4A and B, Table 2-1). These similarities may arise from

the comparison of two equally unimpacted (by humans) areas. Moll (1977, 2006) found that the community composition within an impacted river changed from being predominately specialized turtle species to consisting of mainly generalized turtle species. The higher relative proportion of the generalist *T. s. elegans* and *S. odoratus* observed in the downstream section may be symptomatic of a more heavily-impacted habitat.

Understanding how communities will change in the face of a continuously-shifting environment is ever important as the human population continues to grow (Cohen 1995) and development and alteration of land and waterways are pervasive (Benke 1990, Riccardi and Rasmussen 1999). The relevance of this statement is enhanced in the face of global climate change. Without understanding temporal and spatial variation in communities, it will be difficult to implement effective and efficient conservation and management actions. The need for such data is enhanced for conserving long-lived, imperiled taxa such as turtles.

The North Fork of White River, Ozark County, Missouri and Associated Springs (i.e., Recharge Areas) Are Contaminated with Coliform Bacteria

Contamination of surface water poses threats to ecosystems, wildlife, and human health (Buhlmann and Gibbons 1997, The Nature Conservancy 2003). In areas with porous karst geology, such as the Ozark Plateau, surface water and soil contaminants in recharge areas can flow and seep, respectively, into the groundwater polluting underground aquifers (The Nature Conservancy 2003). Drinking water obtained from contaminated underground aquifers poses a risk to human health (The Nature Conservancy 2003). In Chapter 2, I provided evidence that NFWR and its associated springs are contaminated with coliform bacteria. Levels of total coliform bacteria exceeded limits deemed safe for full body contact by the Missouri Department of Natural Resources (MDNR) in at least one sampling event for all sites sampled during the summer of 2007 (Figure 2-1). *Escherichia coli* levels in all of the springs, downstream sampling

sites, and one upstream sampling site exceeded limits deemed safe for full body contact by MDNR (Figure 2-2). NFWR is a heavily-used river for recreation, including canoeing, tubing, and swimming (Pitt 2005). The excessive levels of coliform bacteria within NFWR pose a risk to human health and may foreshadow high concentrations of other contaminants, such as pesticides and metals. The presence of pesticides has been confirmed in previous studies of NFWR (MDC 2005).

Global Climate Change May Be Enhancing Growth Rates of River Turtles Inhabiting Temperate Climates by Extending the Growing Season and May Be Leading to Earlier Age at Maturity and Age at Size Benefits

Global climate change has been implicated as detrimental to a suite of organisms, including turtles (Root and Schneider 1993, Glen and Mrosovsky 2004, Willette et al. 2005, Parmesan 2006, Hawkes et al. 2007). For turtles, global warming may cause skewed sex ratios of species with temperature-dependent sex determination (Janzen 1994) and decrease the energy reserves of overwintering neonates (Willette et al. 2005). However, turtle physiology is temperature-dependent and increases in environmental temperatures have been linked with increases in growth rates in turtles (Cagle 1946, Gibbons et al. 1981, Rhen and Lang 1995, Roosenburg and Kelley 1996). Increases in growth rate can lead to increased survivorship, earlier sexual maturation, and larger body size at various stages, including maturation (Bury 1979, Thornhill 1982, Cox et al. 1991, Tucker 2000). Larger body size and earlier sexual maturation of turtles can lead to reproductive enhancements such as earlier age at reproduction, increased clutch size, and increased size or quality of eggs (Congdon and Gibbons 1983, 1990, 1996; Lovich et al. 1998).

Analyses of *G. geographica* populations inhabiting the same area during different time periods suggested that the length of the growing season was significantly positively-correlated with instantaneous growth rates of individuals. In Chapter 3, I determined that *G. geographica*

for which sex was visibly indistinguishable (i.e., indeterminate sex) in NFWR in 2004 to 2007 grew approximately 2.8 times faster than similarly-sized turtles in the same section in 1969 to 1972 (Table 3-2). This pattern was significantly correlated with an increased number of growth days in 2004 to 2007 than in 1969 to 1972 (Tables 3-6 and 3-7, Figure 3-1). A comparison of the number of growth days per month revealed that March, April, May, August, and October all had more growth days in 2004 to 2007 than in 1969 to 1972 (Table 3-7). The increased number of growth days in March and October in 2004 to 2007 corresponds with an extension of the growing season as these month mark the boundaries of *G. geographica*'s active season in Missouri (Johnson 2000). Similar results were found by Frazer et al. (1993) for a population of painted turtles (*Chrysemys picta*) in Michigan. These results support the hypothesis that extended growing seasons are positively affecting the growth rate of small juvenile turtles.

In Chapter 4, I demonstrated that male *G. geographica* in NFWR in 2005 to 2007 were growing faster and attaining asymptotic size more rapidly than those in 1969 to 1972 (Figure 4-6). Differences in size-at-age suggest that male *G. geographica* in 1969 to 1972 took twice as long to mature as those in 2005 to 2007 in NFWR. However, male *G. geographica* may have matured at smaller sizes and the same age in 1969 to 1972 than in 2005 to 2007. Regardless, male *G. geographica* in NFWR in 2005 to 2007 would benefit from augmented growth rate leading to earlier age at maturity or larger size-at-age. Earlier maturation is linked with increased lifetime reproductive output (Gibbons et al. 1981) and larger body sizes are associated with greater survival (Gibbons et al. 1981, Janzen 1993, Bodie and Semlitsch 2000, Janzen et al. 2000, Tucker 2000). Therefore, male *G. geographica* in NFWR are benefiting from extended growing seasons in terms of enhanced growth rate. Male *G. geographica* may also be benefiting

from reproductive and/or age-specific survival enhancements. Not enough data were available for female *G. geographica* from 1969 to 1972 to evaluate if patterns were similar between sexes.

Global climate change is resulting in overall warming trends (Schlesinger and Jiang 1991, Manabe and Stouffer 1993, Intergovernmental Panel on Climate Change 2007) and the impacts of global warming on ecosystems and their component communities and populations must be elucidated. Global climate change models predict earlier onset of spring and summer thermal regimes and warmer temperatures (Gates 1993, Intergovernmental Panel on Climate Change 2007). These predictions are consistent with climatic patterns observed in this study. If global climate change is responsible for the observed extended growing seasons, global climate change may be enhancing the growth rate of *G. geographica* within NFWR and I expect similar patterns may be occurring for other temperate river turtle species as global warming is pervasive and turtle physiology is relatively predictable. However, the observed extension in growing season may be due to natural variation rather than global climate change. Regardless of the cause of climatic variation observed within this study, the knowledge gained will be useful for predicting how populations of *G. geographica*, and perhaps other temperate freshwater turtle species, will respond to a rapidly changing climate.

Recommendations

Assess Turtle Communities for Shifts from Predominately Specialist Species to More Generalist Species

North America supports diverse freshwater turtle communities, yet few have received more than a passing account of species presence (Ernst et al. 1994, Moll and Moll 2004). This study revealed that turtle communities can be dynamic and changes in community composition and heterogeneity can coincide with habitat degradation. Symptoms of declining water quality, such as excessive bacterial concentrations and vegetation growth, coincided with an increase in

generalist turtle species. Moll (1977, 2006) observed similar patterns in the turtle community inhabiting the Illinois River. Typically, small, short-lived organisms, such as aquatic macroinvertebrates, are used as indicator species of environmental degradation and biomonitoring (Lenat and Barbour 1994), but the use of long-lived species, such as turtles, may provide information more relevant to other long-lived species, such as humans. Additionally, turtles are imperiled worldwide and the consequences of species losses are poorly understood. Monitoring turtle communities can provide insights into what changes are happening and the effects of these changes.

A major limitation in monitoring long-lived species is that studies must be long-term. To confound issues further, turtle populations are declining worldwide (Smith 1979, Moll 1986, Kuchling 1988, Ernst et al. 1994, Buhlmann and Gibbons 1997, Gibbons 1997, Haitao 2000, van Dijk et al. 2000) and most rivers are excessively modified (Lydeard and Mayden 1995, Ricciardi and Rasmussen 1999). However, information exists in the form of museum collections and historical species accounts, so some information can be gleaned from careful examination of such records (Moll and Moll 2004). Additionally, data that has never been published often exists in the form of field notebooks hidden away in offices or storage (personal observation). In a time of monumental species declines and losses, it is imperative that collaborative efforts be made to exhume these data sets, reassess communities previously studied, and publish the results of these efforts.

Assess Competitive Interactions and Ability between Generalist and Specialist Turtle Species

The turtle community in NFWR changed in composition and heterogeneity between 1969 and 2005, yielding an increased relative and absolute abundance of the generalist species *T. s. elegans* and *S. odoratus* (Figure 2-3A). Between 1980 and 2004, the number of permanent

basking structures (i.e., rocks) declined in NFWR (Pitt 2005). Basking is necessary for thermoregulation, digestion, maintenance of integumentary health, vitamin D synthesis, and parasite removal (Hutchison 1979, Vogt 1979, Hart 1983, Saumure and Livingston 1994, Vogt and Benitez 1997). Many species of turtles bask and I observed all present species except *M. temminckii* basking at least once during the study period (Table 2-2).

Niche overlap measurements indicated a significant overlap in basking habitat use among turtle species in NFWR (Table 2-4). High niche overlap can result from shared resource utilization instigated by lack of competition or intense competition that has not yet resulted in resource partitioning (Pianka 1976).

Niche breadth analysis revealed that *G. geographica* frequently used rocks and logs as basking substrates in 1969 to 1972, but in recent years had increased its niche breadth (Tables 2-2 and 2-3). *Trachemys scripta elegans* and *S. odoratus* were most commonly observed basking on vegetation (Table 2-2). Niche breadth analysis revealed that *S. odoratus* was a basking habitat specialist using vegetation almost exclusively in the downstream section in 2005 to 2007 (Tables 2-2 and 2-3).

I suspect that competition was responsible for the observed patterns of basking habitat use, with *G. geographica* being a better competitor than *T. s. elegans* and *S. odoratus*. However, no aggressive interactions were observed among these species in this study. With the potential for increased numbers of generalist species in systems with degraded habitats, I suggest that competition among turtle species be thoroughly assessed in order to predict subsequent impacts of these community changes.

Conduct a Thorough Assessment of Water Quality in NFWR

The majority of rivers worldwide have undergone massive alterations (Lydeard and Mayden 1995, Ricciardi and Rasmussen 1999) and declines and extinctions of aquatic species

are common (Ricciardi and Rasmussen 1999). Coliform bacteria analyses indicated that NFWR and its associated springs were highly contaminated, posing a risk to human health. The establishment of silt and sediment deposits in NFWR indicated that development and associated storm runoff altered the river's substrate and allowed emergent vegetation stands to grow. Pesticides have also been detected in NFWR (MDC 2005). I recommend a thorough examination of water quality in NFWR and its associated springs. I also recommend that turtles be examined for bioaccumulation of toxins to reveal long-term patterns of contaminant exposure. In addition, I suggest that development along NFWR be evaluated and regulated by state officials to prevent unnecessary runoff and septic contamination of the river. At the same time, landowners should be encouraged to restore and maintain native vegetation in riparian zones to reduce runoff.

Conduct a Comprehensive Assessment of Global Warming's Affects on River Turtles

Results of this study suggested that global warming or climatic variation that is consistent with predictions of global climate change models may be positively affecting turtle growth rates which may have additional benefits including earlier age or larger size at maturation. However, previous studies of global warming's affects on temperature-dependent sex determination in turtles suggested that global warming was feminizing turtles which would reduce recruitment in subsequent generations as male turtles would be rare (Janzen 1994). Additional studies have also suggested that reptiles, such as turtles, are not mobile enough to undergo range shifts through fragmented habitats in the face of a rapidly changing climate (Araujo et al. 2006). Global warming may also reduce energy stores of overwintering hatchling turtles that remain in the nest (Willette et al. 2005). Reduced energy reserves may negatively impact survival rates (Willette et al. 2005) I suggest that comprehensive studies of global warming's affects on turtles

be conducted in many parts of the world and with diverse species as climate change is predicted to affect various locations differently, especially in terms of water resources (Arnell 1999).

Assess the Relative Importance of Temperature versus Length of Growing Season on Turtle Growth

Phenotypic plasticity in traits, such as growth rate, that can directly influence life history parameters is important for organisms inhabiting variable environments (Caswell 1983, Stearns and Koella 1986). For turtles and other ectotherms, temperature is an influential abiotic factor that can alter phenotypic traits that directly modify life history parameters (Laudien 1973, Lillywhite et al. 1973, Gibbons et al. 1981, Bronikowski et al. 2001). Temperature has been positively correlated with growth rate of turtles (Cagle 1946, Gibbons et al. 1981, Rhen and Lang 1995, Roosenburg and Kelley 1996). Enhanced growth rate has been correlated with increased survivorship, earlier sexual maturation, and larger body size at various stages, including maturation (Bury 1979, Thornhill 1982, Cox et al. 1991, Tucker 2000). Earlier sexual maturation and increased body size has been linked with increased lifetime reproductive output (Congdon and Gibbons 1983, 1990, 1996; Lovich et al. 1998).

Comparisons of turtle populations inhabiting thermally-distinct habitats have been conducted to assess the impact of power-plant effluents on turtles (Parmenter 1980, Thornhill 1982, Spotila et al. 1984). Studies have implicated temperature as a factor influencing turtle growth rate and size and age at maturity (Parmenter 1980, Gibbons et al. 1981, Thornhill 1982).

In Chapter 3, I determined that *G. geographica* inhabiting two sections of a spring-fed river with significantly different thermal regimes did not exhibit differences in mean instantaneous growth rate (Table 3-3). This result was unexpected as similar differences in water temperature at other sites have been implicated as contributors to variation in turtle growth rates

(Parmenter 1980, Thornhill 1982). The discrepancy in results between this study and others suggest that difference in temperature alone cannot increase turtle growth rate.

Studies in which differences in growth rate were observed among turtles had the commonality of increased length of the growing season (Thornhill 1982). I hypothesized that the discrepancy in temperature between the two sites may be counteracted by the downstream section having an extended growing season relative to the upstream section. I proposed that the spring effluents buffer the water temperature of the downstream section while the water temperature of the upstream section varies naturally with air temperature. This buffering effect could increase the growing season of the downstream section relative to the upstream section, especially for basking species that overcome the constraints of their aquatic thermal environment. I suggest that controlled experiments be conducted to assess whether differences in water temperature alone can influence turtle growth rate if all other variables are held constant and food is not limiting. Not only would this proposed experiment clarify factors that influence turtle physiology, but it would further elucidate the mechanism behind how global warming may affect turtle growth rate. I also recommend evaluating the active season of turtles inhabiting different sections of NFWR to confirm or refute whether growing seasons vary in length among areas with differing thermal regimes.

Continue Monitoring the Turtle Community in NFWR to Provide Insight Regarding the Continued Impacts of Climatic Variation and Habitat Alterations on Turtle Communities

Few studies provide data from several decades and long-term monitoring is necessary to observe temporal variations in populations and communities. As development, pollution, and climate change are omnipresent, it is imperative to determine how these factors will impact communities and ecosystems over both short and long-term timescales. The dearth of long-term studies must be overcome to adequately predict how various influences will impact communities.

The few communities and populations from which long-term data are available provide unique insights and opportunities for assessing continuous changes to the environment. Therefore, I recommend that the turtle community in NFWR continue to be monitored for many more decades.

Final Remarks

The turtle community in NFWR presents a unique opportunity to assess changes in turtle populations, communities, and habitats in the face of riparian development and climatic variation. As few long-term data are available to assess turtle communities and populations and turtles are imperiled worldwide, we must take advantage of the few opportunities we do have to study these communities and populations if we wish to document changes that are occurring in association with human-borne environmental changes. Without this documentation, it is unlikely that financial, political, and public support of turtle conservation will improve.

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BIOGRAPHICAL SKETCH

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