

**The Potential for Competition Between the Red-bellied Turtle
(*Pseudemys rubriventris*) and the Red-eared Slider Turtle
(*Trachemys scripta elegans*)**

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Dedications

To Ruby Shayna Eckstein who taught me much about life and love during her short stay with us.

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Abstract

The Potential for Competition Between the Red-bellied Turtle (*Pseudemys rubriventris*)
and the Red-eared Slider Turtle (*Trachemys scripta elegans*)

Steven Henry Pearson

Invasive species are a significant cause of biodiversity declines on a global scale and novel species interactions often cause ecological damage through predation or competition. The red-eared slider turtle (*Trachemys scripta elegans*) has been introduced to wetlands globally and negatively impacts other native turtle species. In Pennsylvania, USA, the red-eared slider turtle is ecologically similar to the PA, state threatened red-bellied turtle (*Pseudemys rubriventris*). The objective of this dissertation is to examine the potential for competition between red-eared slider turtles and red-bellied turtles using field studies of adult free ranging turtles and manipulative studies of juvenile turtles in mesocosms. Field studies utilized intensive trapping, radio telemetry, stomach flushing, fecal sample collection and stable isotopes to determine populations sizes, spatial resource use and dietary resource use of both species. Intensive trapping and radio telemetry revealed that both species used wetland habitats ubiquitously. Dietary studies revealed that at a smaller, more highly fragmented and vegetative species depauperate wetland complex, red-eared slider turtles and red-bellied turtles overlapped extensively for dietary resources while at a larger, intact, more vegetative species rich wetland the diets of both species were partitioned. In manipulative experiments in which red-eared slider turtles and red-bellied turtles were housed in low resource availability groups and high resource availability groups with conspecifics or in mixed species groups red-eared

slider turtles were competitively superior to red-bellied turtles. Field study results suggest that the potential for competition between red-eared slider turtles and red-bellied turtles varies depending on local habitat characteristics, while manipulative experiment results suggest that red-eared slider turtles are competitively superior in resource limited environments. These results combined suggest that in degraded wetland habitats, when resources become limited, red-eared slider turtles will have a competitive advantage over red-bellied turtles potentially leading to population declines. Red-eared slider turtles should not be sold outside of their native range as pets and when possible they should be removed from wetland habitats outside of their native range. Furthermore, wetland habitats should be managed and preserved to provide intact, species rich and species diverse habitats.

CHAPTER 1: General Introduction

Threat of Habitat Degradation to Biodiversity

Habitat degradation and invasive species are the first and second greatest causes of extinctions and population declines worldwide respectively (Wilcove et al. 1998). Both, habitat degradation and invasive species cause the decline of native species individually but synergistically they further exacerbate population declines. Habitat degradation destroys or renders habitats unsuitable and limits the resources available to individuals. Limiting resource availability can increase the extent of resource overlap between individuals and species, oftentimes decreasing niche breadth (Swihart et al. 2003b, Luiselli 2006). In addition to altering resource availability, degraded habitats are ideal environments for the establishment of invasive species populations as a result of altered community composition and undeveloped community structure; in recently disturbed or recovering habitats, there are open niches that can be filled by either native species or non-native species (D'Antonio and Vitousek 1992, Mack et al. 2000b). Invasive species alter community composition of ecosystems and negatively impact native species through predation and competition (Alison et al. 1995).

On a global scale, habitat loss is the leading cause of extinctions and population declines and is attributed to causing population declines for 85% of all endangered species (Wilcove et al. 1998). On a local and regional scale habitat degradation can have both positive and negative impacts on the local biodiversity depending on the community's response to disturbance (Fahrig 2003). When discussing habitat degradation it is important to consider the disturbance regime of that habitat. The disturbance regime is the extent of habitat disturbance coupled with the frequency of disturbance occurring at a given site (D'Antonio and Vitousek 1992). Differences in

disturbance regimes may cause decreasing levels of biodiversity found across a disturbance gradient, with larger, more frequent disturbances resulting in decreased biodiversity (Swihart et al. 2003a). As the level of anthropogenic disturbance grows, there may be a decrease in available resources, leading to an increase in resource overlap between species and a narrowing niche breadth (Swihart et al. 2003b, Luiselli 2006). As resource overlap increases between species the risk of any one resource becoming limited also increases creating a greater potential for competition to occur (Bellgrah et al. 2008). The potential for inter-specific competition may be greater in highly degraded ecosystems that contain fewer resources.

Threat of Invasive Species to Biodiversity

Invasive species have contributed to the population decline of many species globally. In the United States at least 42% of species protected under the Endangered Species Act are protected due to the impacts of invasive species (Pimentel et al. 2005). On regional scales invasive species have been linked to 80% of endangered species listings (Pimentel et al. 2005). The two main mechanisms that cause the decline of population sizes by invasive species are predation on native species and competition with native species (Alison et al. 1995). Increased rates of predation occur when native species are unaccustomed to predation or can no longer adapt quickly to elevated rates of predation (Fritts and Rodda 1998). Introduced predators can cause the severe collapse of native faunas due to an increase in the predation rates imposed on native species (Schoener and Spiller 1996, Rodda et al. 1997).

Introduced species also cause the decline of native species through increasing the rates of exploitative and interference competition (Polis and McCormick 1987,

Amarasekare 2002). Competition between native and introduced species negatively impact native species by causing reduced growth rates, reproductive rates and/or survival rates (Polis and McCormick 1987). Alterations in the growth rates, reproductive rate or survivorship must be shown to occur in the presence of a competitor to demonstrate that competition has a role in shaping community structure (Polis and McCormick 1987, Amarasekare 2002).

In many long-lived, slowly maturing organisms, small size classes are ideal to study competitive interactions due to their quick rate of growth. In addition to the benefit of using smaller size classes for short term studies, there are biologically significant reasons to study developmental rates of juvenile turtles. In many reptiles body size has been shown to be highly correlated with long-term reproductive success in both size of offspring and in the total potential number of offspring produced; this is seen in snakes (Luiselli et al. 1996), crocodylians (Thorbjarnarson 1994) and in turtles (Dunham and Gibbons 1990, Gibbons 1990b, Rollinson and Brooks 2008). The growth rates of juvenile reptiles may therefore have lifelong consequences for the reproductive output and overall fitness of individuals.

Factors Influencing Invasions

There are several main hypotheses and mechanisms that are involved in determining the success of biological invasions in novel environments that include both biotic and abiotic factors. The major biotic factors that influence the success of an introduced species are the propagule pressure, the characteristics of the species being introduced (i.e. dietary and habitat needs), and the community dynamics/species composition at a release site. (D'Antonio et al. 2001, Lockwood et al. 2007). The

disturbance regime at a release site is a significant abiotic factor that can be useful in predicting success of a species invasion (Herbold and Moyle 1986, deRivera et al. 2005, Lockwood et al. 2007).

Propagule pressure is an important biotic feature in determining the success of an introduced species. The propagules are “the set of individuals released in to the environment” (Lockwood et al. 2007). The propagule pressure is created by the number of individuals introduced, physical condition of individuals and the frequency of introductions that occur (Lockwood et al. 2007). As the propagule size increases, the probability of an introduced species surviving stochastic events (e.g. drought or flood) also increases (Lockwood et al. 2007). Smaller propagule numbers are likely to increase the Allee effects that introduced populations must survive through. Examples of Allee effects that introduced species may be exposed to are limited opportunities for finding mates and decreased foraging capabilities (Lockwood et al. 2007).

The physical condition of the propagules and the environmental conditions, such as environmental temperature present at an introduction site, are also extremely crucial in the success of a species initial invasion. If the physiological requirements needed for the survival of a species are not met in their new environments a potential invader will be unable to successfully establish itself (D'Antonio et al. 2001, Lockwood et al. 2007). The effects of propagule size are often dependent on a community's ability to resist invasion. A community can resist invasion through having a well-structured community with few open niches, abundant native predators or strong native competitors (Herbold and Moyle 1986; deRivera, Ruiz et al. 2005). A community's defense in deterring invasions is termed the community's biotic resistance (Von Holle and Simberloff 2005). When biotic

resistance is low it takes very few propagules to establish and successfully invade an ecosystem (Herbold and Moyle 1986, deRivera et al. 2005, Lockwood et al. 2007).

However, when biotic resistance is high, a high level of propagule pressure is needed for successful establishment (D'Antonio et al. 2001).

There are no characteristics that describe all successful invasive species (Mack et al. 2000b). However, many successful invasive species exhibit rapid population growth (Rejmanek and Richardson 1996). Rapid population growth can occur due to life history traits (e.g. early sexual maturity, frequent reproduction, and small offspring size), through a large initial propagule size or through repeated release events (Rejmanek and Richardson 1996, Lockwood et al. 2007). Rapid population growth allows for invading species to take advantage of favorable conditions present during the period of introduction. Populations that grow quickly are capable of successful establishment prior to a shift in environmental conditions or before a community develops increased biotic resistance (Alpert 2006).

In addition to propagule size and the life history traits discussed, competitive ability of introduced species may play a role in the successful invasion of introduced species. The capabilities of an introduced species to successfully out-compete and/or resist the competition exerted by already present, ecologically similar species is an important factor in determining the success of a species invasion (Duyck et al. 2007). In habitats with ecologically similar species the probability that overlap for resources will occur is greatly increased (Collins et al. 2007). An increase in the amount of resource overlap creates the potential for competition between an introduced species and a native species.

One major abiotic factor in determining a successful invasion is the disturbance regime at a given location (Mack et al. 2000b). An ecosystem's susceptibility to invasion is heavily influenced by natural disturbances (e.g. floods and -fire) and anthropogenic disturbances (e.g. livestock grazing and habitat alteration) prior to and at the time of propagule release (D'Antonio and Vitousek 1992, Mack et al. 2000b). Increased levels of disturbance are often correlated with decreases in resource availability for some species. This decrease in available resources can lead to a narrowing of a species niche breadth (Luiselli 2006). The reduction of available resources can also increase the extent of resource overlap with potential competitors (Swihart et al. 2003b, Luiselli 2006). When the resource base narrows and the amount of overlapping resources between species increases, the potential for competition between species also increases.

Additional causes of an ecosystems susceptibility to invasion have been outlined as hypotheses that can often explain most of successful invasions. These hypotheses are shown in Table 1.

The hypotheses described in Table 1 all involve competition in some manner. Competition plays an important role in deterring potential invasive species as well as impacting native species after a species has invaded successfully. The role that a successful invader plays within an ecosystem is of profound importance to the subsequent survival of native species within the introduced species' novel range.

Invasive Species in Novel Environments

Invading species can negatively impact the vital rates of native flora and fauna. The most obvious negative impact on native species is the direct cause of mortality due to predation. Introduced predators are known to have decimated populations as well as

entire faunas of naïve prey sources (Schoener and Spiller 1996, Rodda et al. 1997, Davis 2003). To determine the impacts that introduced species have on native species populations it is necessary to understand whether an introduced species might potentially compete with native species and how competition might negatively affect native species.

If competition between species occurs the resources used by competing species are altered, narrowing the breadth of a species realized niche, and impacting the growth, survival and reproduction of either species (Polis and McCormick 1987). The fundamental niche is defined as all of the environmental and resource dimensions that a species can survive and reproduce in (Austin et al. 1990). Within an established community, species obtain a realized niche (i.e. a subset of the fundamental niche where a species has a competitive advantage), to partition available resources and limit the extent of resource overlap between species (Austin et al. 1990, Shea and Chesson 2002). When considering the niche space of a species it is important to consider all aspects of an organism's life including dietary, spatial and temporal niche space. The overlap of resources that occurs between native species and introduced species may result in an alteration of a native species realized niche (Austin et al. 1990, Shea and Chesson 2002).

Competition between species can be either exploitative or through interference. Exploitative competition occurs when an organism depletes the resources that a second species would otherwise consume. Interference competition occurs through direct interactions for spatial resources limiting an individuals or species access to that resource (Begon 1986, Morin 1999).

To determine if competition occurs between native and introduced species, both exploitation and interference competition need to be considered (Amarasekare 2002).

Polis and McCormick (1987) outline the conditions that must be occur for exploitation competition to exist by describing the resource limitation condition and the resource depletion condition (Polis & McCormick 1987).

The resource limitation condition exists when resource levels affect the growth, survival and/or reproduction of a species. To demonstrate the resource depletion criteria, one must demonstrate that under increased resource availability, the rates of growth, reproduction, and/ or percent feeding increase. This condition states that lower performance or abundance of one species is clearly caused by the presence or absence of a second species. This condition is met when resource depletion suppresses the growth rates, immigration rates, survival rates or reproductive rates of a species (Polis & McCormick 1987).

Interference competition can be determined through measuring a consumer's ability to exploit resources along a resource availability gradient (Amarasekare 2002). For both exploitative and interference competition to occur, an overlap for potentially limited resources must occur. Furthermore, for exploitative and interference competition to occur simultaneously, all conditions must be met (Amarasekare 2002).

Determining the potential for competition between species using resource overlap

Major resource categories in which competition may occur between species are dietary and spatial resources. Spatial overlap between species must occur for competition between species to also occur. If species do not coexist in the same environments then competition between those species is non-existent. Resource overlap for food may negatively impact the amount or quality of food consumed over time. These impacts on quantity and quality of food consumed may negatively impact the growth, survivorship

and reproduction of the species competing for these resources. Techniques used to determine spatial overlap between species include capture-mark-recapture techniques, telemetry and observational techniques. Capture-mark-recapture techniques are important for studying whole populations of organisms and enable the determination of population demographics of study organisms. Through individual identification and repeated captures an understanding of a populations structure, size and distribution can be used to manage for the continued survival or recovery of a species (Mills 2008). Similarly, radio telemetry is used to gain information on individual habitat use (Roe and Georges 2008, Franks et al. 2011) and observations can be used to determine a species distribution (Stone 2010, Thomson et al. 2010). These three techniques are commonly used to determine the distribution, abundance and the habitat use of a wide variety of taxa (Mills 2008).

Techniques used to determine dietary resource use of organisms include fecal analysis (Jensen and Das 2008), stomach flushing which is a minimally invasive technique (Legler 1977, Parmenter and Avery 1990, Lindeman 2000, Chen and Lue 2009), and stable isotope analysis (Reich et al. 2007). Fecal collection and stomach flushing are useful tools for gaining insight into the dietary items that are consumed by a species. The major flaw with these techniques is that they are inconclusive in determining the entire resource base being consumed by the species being studied. Dietary items that are digested at higher rates or more completely digested are often underrepresented in samples of stomach contents, while more slowly digested items may appear more abundant.

Carbon and nitrogen stable isotopes are often used to study trophic interactions (Peterson and Fry 1987, Bluthgen et al. 2003, Bulte and Blouin-Demers 2008). The delta ^{15}N and delta ^{13}C isotopes can be used to determine both the trophic level that an organism belongs and the source of carbon that the organism feeds on (Post 2002). The premise of all stable isotope studies are that isotopes are incorporated into an object, whether it be during rock formation or through an organism feeding on its prey base (Fry 2006). Nitrogen and carbon stable isotopes are incorporated into tissue during physiological processes (Kilham et al. 2009). The delta ^{15}N and delta ^{13}C isotope content are dependent on many of the factors that affect the assimilation of isotopes, including tissue metabolism, trophic level, environmental conditions, the C:N ratios in the food items being consumed, temperature taxonomy, body size and an organisms method of eliminating nitrogenous waste (Vanderklift and Ponsard 2003, Kilham et al. 2009); other factors also exist.

Significance to Freshwater Turtle Communities of Pennsylvania

Red-eared Slider Turtle

The red-eared slider turtle, *Trachemys scripta elegans* is a species that is widely distributed outside of its native range. Repeated introductions has created high propagule pressure resulting in the red-eared slider turtles being one of the world's most widespread non-native aquatic vertebrates, occupying ecological niches in wetlands on all continents except Antarctica (Lever 2003). The native range of the red-eared slider turtle is in the Mississippi River Valley from Illinois southward to the Gulf of Mexico (Ernst et al. 1994). This species is a nutritional and habitat generalist that can survive in multiple habitat types (Gibbons 1990a, Parmenter and Avery 1990) which allows for adaptation to

a novel environment's available resources (Marvier et al. 2004). In its native range, the red-eared slider turtle prefers lacustrine habitat (i.e. slow moving deep water) over riverine habitats (i.e. fast moving) and shifts from an omnivorous diet to near herbivory as adults (Parmenter and Avery 1990, Ernst et al. 1994, Stone 2010). In addition, studies suggest that red-eared slider turtles may compete with native turtle species for limited spatial, temporal and dietary resources (Cadi and Joly 2003, 2004).

In North America, red-eared slider turtles have been reported as introduced in 24 states within the United States and 2 provinces of Canada that are outside of its native range (Somma et al. 2009). The northeastern and mid-Atlantic states of the United States have not been exempt from receiving its share of naturalized red-eared slider turtle populations. Naturalized populations exist in all coastal and near coastal states between Maine and South Carolina (Somma et al. 2009).

Red-bellied Turtle

The red-bellied turtle, *Pseudemys rubriventris*, is a turtle species native to the mid-Atlantic coastal region of the United States and is found continuously southward from central New Jersey to the northeastern part of North Carolina. Several relict populations exist in Massachusetts (Waters 1962, Ernst et al. 1994). The decline of red-bellied turtle populations has been ongoing throughout recent history (Waters 1962). The historic population of red-bellied turtles ranged continuously between New England and Virginia (Waters, 1962). With the exception of the disjunct Massachusetts populations, red-bellied turtles had been extirpated in the northern part of its historical range by the late 1800's when they were extirpated due to over-harvesting (McCoy 1985). Throughout the late 20th century and early in the 21st century populations of red-bellied

turtles appeared to decline within the northern limits of its current range. In Pennsylvania, the red-bellied turtle has been protected since 1978 and recent research by Avery et al. (2010) suggest that this species has been lost from over 50% of the sites where it was historically found (Hulse 2001 , Avery et al. 2006, Stone 2010). Historic causes of the red-bellied turtle decline are over-harvesting, habitat loss and environmental degradation or pollution (Ernst et al. 1994, Hulse 2001). In addition to the historic causes of red-bellied turtle population declines, repeated introductions and the establishment of red-eared slider turtle populations may be a cause of the continued decline of red-bellied turtles in the northern limit of its current range.

Potential impacts of red-eared slider turtles on red-bellied turtles

Red-eared slider turtles may be a cause for the continued decline of red-bellied turtle populations due to the similarities reported for dietary and spatial needs. Dietary and spatial resource overlap can occur between native turtles and introduced red-eared slider turtles wherever they are introduced due to the red-eared slider turtle's generalist nature (Gibbons 1990a, Parmenter and Avery 1990, Cadi and Joly 2004). By quantifying the extent of resource overlap between red-eared slider turtles and red-bellied turtles, we can examine potential mechanisms that allow these two species to coexist while better understanding the role that red-eared sliders may be playing in the decline of red-bellied turtle populations.

The diets and nesting requirements of red-eared slider turtles and red-bellied turtles are expected to overlap (Ernst et al. 1994, Stone 2010). Both species are omnivores as juveniles with pronounced shifts towards herbivory at larger size classes.

Both species have similar nesting seasons and preferred nesting substrates (Ernst et al. 1994, Stone 2010).

Study Sites

Throughout the text of this dissertation readers will be referred to the names of wetland complexes and to the individual wetlands within those complexes. These individual wetlands are detailed below. These sites were chosen due to their locations, the presence of both red-bellied turtles and red-eared slider turtles and a history of turtle research occurring at these sites.

The Wetlands at Fort Mifflin

The wetland complex at Fort Mifflin (FM) is comprised of four different wetlands. These four wetlands are the Delaware River at Fort Mifflin, EMC-10, EMC-11 and the Moat at Fort Mifflin. For this study I considered the Delaware River at Fort Mifflin as the embayment found adjacent to the Moat at Fort Mifflin. Wetlands EMC-10 and EMC-11 are located adjacent to Hog Island Road and the entrance to Fort Mifflin. The Moat is dug impoundment that surrounds the fort. The Moat is divided into an east and a west side by narrow patches of land.

Wetlands at the Silver Lake Nature Center

The wetland complex at the Silver Lake Nature Center (SLNC) is comprised of five different wetlands. These five wetlands were Silver Lake, Mill Creek, Magnolia Lake, the Unconnected Pond and North Mill Creek. Silver Lake was considered all of Silver Lake from Rt. 13 in the southern end north to where the Lake narrows out and becomes channelized. Mill Creek began at the channel that opened up to Silver Lake and continued north under Lakeland Avenue and dissipated in a narrow shallow channel that

led northward. Magnolia Lake on its southeastern shore began at an opening from Mill Creek just north of Lakeland Avenue and was bordered on the south by Lakeland Avenue, on the west by Oxford Valley Road and on the North and East shores by undeveloped parkland. The Unconnected pond was a shallow pond that was along the northern shoreline of Magnolia Lake. Magnolia Lake and the Unconnected Pond were separated by a narrow strip of land. North Mill Creek was the section of creek that flowed into Magnolia Lake from the north ending at the Pennsylvania Turnpike bridge.

Research Questions and Dissertation Structure

Invasive species are a major concern on all continents because they negatively impact the distribution and abundance of native species through predation and competition. In Pennsylvania the red-eared slider turtle is an invasive species that may negatively be impacting the abundance and distribution of the ecologically similar, state threatened red-bellied turtle. The goal of this dissertation was to determine the extent of resource overlap between wild populations of red-eared slider turtles and red-bellied turtles and to determine if red-eared slider turtles could negatively impact red-bellied turtles in resource limited conditions. The specific research questions in this dissertation are

1. What is the extent of spatial overlap between red-eared slider turtles and red-bellied turtles in wetlands in which they coexist?
2. What is the extent of dietary resource overlap between red-eared slider turtles and red-bellied turtles in wetlands in which they coexist?
3. Do red-eared slider turtles negatively impact the growth rates of red-bellied turtles in experimental resource limited environments?

These questions are each addressed in separate chapters of this dissertation. Chapters two and three detail the field studies components of the dissertation. Chapter two examines the abundance of the entire turtle community found in the study wetlands. In addition to abundance data for each species special attention is paid to the distribution and general spatial resource use of red-eared slider turtles and red-bellied turtles throughout the wetlands at Fort Mifflin and those at the Silver Lake Nature Center. The third chapter details the extent of dietary overlap, as determined by stable isotopes analyses, between red-eared slider turtles and red-bellied turtles and relates resource overlap to metrics of resource availability such as wetland size, species richness and species diversity. The fourth chapter details the manipulative experiment that was performed to determine whether or not red-eared slider turtles can negatively impact the growth of red-bellied turtles. In chapter five the results of the field studies and manipulative experiments are summarized, related to one another and utilized to suggest management strategies that could reduce the impact of red-eared slider turtle introductions. In addition to the main chapters of the dissertation I have included an appendix that contains the results of trapping data and abundance estimates for all of species in all of the wetland complexes that I collected data.

Table 1-1. Major hypotheses that may explain an invasive species successful invasion.

Global Competition Hypothesis	Introduced species succeed because the number of possible species to be introduced far exceeds the number of native species present. An extension of this hypothesis states that ecosystems with a smaller number of native species should be more invisable than ecosystems with a larger number of native species (Alpert 2006).
Naturalization Hypothesis	Introduced species that are functionally different than native species will have a better chance of establishing successfully. Functionally different species benefit through introductions by a decreased likelihood of pathogens and predation on the introduced species (Ricciardi and Mottiar 2006).
Empty Niche Hypothesis	A greater functional difference between introduced and native species increases the likelihood of successful establishment (Darwin 1859, Von Holle and Simberloff 2005). An extension says that community species richness has an important role in deterring invasions (Elton 1958). A well-maintained community with numerous species will have few empty niches (Mack et al. 2000b).
Stochastic Niche Theory	As propagule number increases the chance of successful invasion also rises. This theory considers the impacts of demographic stochasticity, the mechanisms of competition, and the constraints that invading species must be able to survive, grow, and reproduce using the resources available to them (Tilman 2004)
Enemy Release Hypothesis	Introduced species are without their “native associates” (i.e. Competitors, predators, grazers, and parasites from its native range). Species that have escaped from their native associates are able to excel at many fitness levels (Mack et al. 2000b)

CHAPTER 2: Invasive red-eared slider turtles (*Trachemys scripta elegans*) overlap for spatial resources with native red-bellied turtles (*Pseudemys rubriventris*)

Introduction

An organism's habitat use is defined by landscape features that determine the overlap between the physical space available to obtain all of the resources necessary for growth, reproduction and survival, the density of those resources, the biophysical limits of the space and the biotic interactions that limit the activity of that organism (Porter and Gates 1969, Hall et al. 1997, Krausman 1999). The full set of habitats and resources within which an organism can exist is considered the fundamental niche for that organism (Begon et al. 2006). Interactions between abiotic factors and biotic factors that lead to limitations in an organism's actual habitat and resource use determine the realized niche for that organism (Austin et al. 1990, Shea and Chesson 2002). By determining the site specific habitat use of a species I can begin to understand how that species utilizes the environment in relationship to the entire community.

In naturally evolved, well-structured communities few open niches should exist due to the presence of native predators or strong native competitors (Herbold and Moyle 1986; deRivera, Ruiz et al. 2005). The level of biotic resistance (i.e. defenses to deter invasions) within a community may be an important factor determining if a novel species can become naturalized in the environment (Von Holle and Simberloff 2005). When biotic resistance is low, novel species can successfully invade an ecosystem (Herbold and Moyle 1986, deRivera et al. 2005, Lockwood et al. 2007). However, when biotic resistance is high, successful establishment of invasive species is difficult (D'Antonio et al. 2001). An ecologically similar, competitively dominant, novel species may be able to overcome the high levels of biotic resistance and successfully invade an ecosystem. One

way to determine if a species has successfully naturalized or invaded a habitat is to look at its local and regional distributions, abundance and density.

At a regional scale broad establishment of a species infers that the species has at least been introduced on many occasions and likely has been able to increase population size through reproductive means (Lockwood et al. 2007). On a local scale more detailed studies of how a species utilizes the environment can be useful in determining the impacts of an introduced species on native species (Adams et al. 2013). Introduced species impact native species mainly through predation on native species and competition with native species (Alison et al. 1995). Increased rates of predation occur when native species are unaccustomed to predation or cannot adapt quickly to elevated predation rates (Fritts and Rodda 1998). Introduced predators can cause the severe collapse of native faunas due to increased predation rates imposed on native species (Schoener and Spiller 1996, Rodda et al. 1997). Increased competition between native and introduced species can negatively impact native species through reductions in growth rates, reproductive rates and survival rates (Polis and McCormick 1987, Amarasekare 2002).

In ectotherms, such as turtles, spatial resources which ecologically similar species may compete for include basking sites, foraging sites and nesting sites. A commonly introduced ectotherm on all continents is the red-eared slider turtle (*Trachemys scripta elegans*) (Lever 2003). In wetlands where red-eared slider turtles have been introduced competition for spatial resources has the potential to negatively impact native species (Cadi and Joly 2004). In Pennsylvania, USA, the most ecologically similar species to red-eared slider turtles, with which we might expect resource overlap to occur, is the red-bellied turtle (*Pseudemys rubriventris*). The dietary, nesting and thermoregulatory

requirements for these species are similar (Ernst et al. 1994, Stone 2010). The painted turtle (*Chrysemys picta*) may also be ecologically similar. However, eastern painted turtles are generalists throughout all life stages (Ernst et al. 1994, Hulse 2001).

Red-bellied turtles and red-eared slider turtles share similar dietary characteristics; they both are omnivores as hatchling/juveniles and have pronounced shifts towards herbivory as adults (Clark and Gibbons 1969, Graham 1971, Parmenter and Avery 1990). In terms of thermoregulatory resource use both red-bellied turtles and red-eared slider require large stable basking sites for thermoregulation (Ernst et al. 1994). Thermoregulation is a behavioral adaptation used to regulate the body temperature of reptiles; turtles with higher body temperatures have an increased metabolic rate and in turn digest food and assimilate nutrients at higher rates (Hammond et al. 1988, Avery et al. 1993). Thermoregulation is a key component in assimilating nutrients necessary for growth and reproduction of turtles (Avery et al. 1993). Competition between ectothermic organisms for basking resources may limit the body temperature of one species and result in decreased growth rates and survivorship if body temperatures are reduced (Cadi and Joly 2003, 2004). As adults, red-bellied turtles and red-eared slider turtles are large bodied and cannot utilize emergent vegetation or small floating objects for basking, therefore, they must use solid objects such as fallen logs, emerged rocks or other emergent objects to bask when water temperatures are too low to allow aquatic basking at the waters surface. They typically do not use the shoreline because of the danger of predation. Quality basking sites are not always abundant in wetlands and may be a limiting resource in some wetlands.

In addition to overlapping dietary needs and basking requirements, the nesting season and preferred nesting substrates of these two turtle species are similar (Ernst et al. 1994, Stone 2010). If sympatric red-bellied turtles and red-eared slider turtles utilize the same nesting habitats, then these nesting areas may also be a site for competition between these species.

The objectives of this study were to determine the relative abundances, estimate population sizes and determine general habitat use for red-eared slider turtles and red-bellied turtles at two wetland complexes to determine the potential for competition for spatial resources

Materials and Methods

Study Species

Red-eared slider turtles, (*Trachemys scripta elegans*) are widely distributed outside of its native range and has been documented occupying ecological niches in wetlands on all continents except Antarctica (Lever 2003). The release of unwanted pets has resulted in the red-eared slider turtle being considered one of the world's most widespread non-native aquatic vertebrate (Lever 2003). The red-eared slider turtle's native range is in the Mississippi River Valley from Illinois southward to the Gulf of Mexico (Ernst et al. 1994). Red-eared slider turtles are nutritional and habitat generalist that can survive in multiple habitat types (Gibbons 1990a, Parmenter and Avery 1990). The generalist nature of this species allows it to adapt to novel environments (Marvier et al. 2004). In its native range, the red-eared slider turtle prefers lacustrine habitat (i.e. slow moving deep water) over riverine habitats (i.e. fast moving) and shifts from an

omnivorous diet to near herbivory as adults (Parmenter and Avery 1990, Ernst et al. 1994). Red-eared slider turtles may compete with native turtle species within their introduced range for limited spatial, temporal and dietary resources (Cadi and Joly 2003, 2004).

In North America, red-eared slider turtles have been reported as introduced in 24 states within the United States and two provinces of Canada that are outside of its native range (Somma et al. 2009). The northeastern and mid-Atlantic states of the United States have not been exempt from receiving its share of introduced red-eared slider turtle naturalized populations. Naturalized populations exist in all coastal and near coastal states between Maine and South Carolina (Somma et al. 2009).

Red-bellied turtles (*Pseudemys rubriventris*) are native to the mid-Atlantic coastal region of the United States. The current distribution is between central New Jersey to the northeastern part of North Carolina. Historic populations existed between New Jersey and Massachusetts and several relict populations still exist in Massachusetts (Waters 1962, Ernst et al. 1994). The decline of red-bellied turtle populations has been ongoing throughout recent history (Waters 1962). With the exception of the disjunct Massachusetts populations, red-bellied turtles had been extirpated in the northern part of its prehistoric range by the late 1800's when the New York population of red-bellied turtles were extirpated due to over-harvesting. Red-bellied turtle populations continue to be in decline within the northern limits of its current range. In Pennsylvania, the red-bellied turtle has been protected since 1978 and recent research by Avery et al. suggest that this species has been lost from over 50% of the sites where it was historically found (Hulse 2001 , Avery et al. 2006, Stone 2010). Red-bellied turtle decline has been due to

over-harvesting, habitat loss and environmental degradation or pollution (Ernst et al. 1994, Hulse 2001). In addition to the historic causes of red-bellied turtle population declines, repeated introductions and the establishment of red-eared slider turtle colonies may be a cause of the continued decline of red-bellied turtles in the northern limit of its current range.

Study Sites

I carried out my research at two wetland complexes that differed in size and the extent of connectivity. One wetland complex was located at the Silver Lake Nature Center (SLNC), Bristol, PA. The study site consisted of two large lakes, (Magnolia Lake and Silver Lake) each greater than nine hectares and connected to one another by Mill Creek and surrounded by protected lowland forest and parkland. In addition to the major lakes and connecting creek the greater watershed is 5092 Hectares with most of the drainage being north of Magnolia Lake and is drained by the Mill Creek and it's major tributaries, (Black Ditch Creek and Queen Anne's Creek) (Aqua-Link 2002). At the north end of the study site Mill Creek empties into Magnolia Lake and there is a one hectare pond (Unconnected Pond) to the west of Mill Creek and North of Magnolia Lake. At the south end of the study site, Silver Lake drains over a spill way into Otter Creek which winds to the Delaware River about 2 km to the south. Adjacent and to the east of Silver lake there is a shallow wetland that is connected to Silver Lake through a narrow canal. Furthermore, 500 m downstream from Silver Lake there is a storm-water retention pond adjacent to Otter Creek.

The second wetland complex was at Fort Mifflin (FM), Philadelphia, PA and consisted of three small wetlands (Moat, EMC10 and EMC11), each less than 2 hectares

separated by steep banks and paved roads, and surrounded by mowed lawns and narrow patches of forest. The Moat had an area of 1.6 hectares and is the eastern most wetland located directly adjacent to the Delaware River. The Moat is separated from the Delaware River by a levee. EMC11 had an area of 0.1 hectares and is located to the northwest of the moat separated terrestrially by a steep forested embankment and a chain link fence. EMC10 had an area of two hectares and is located to the north of EMC11. EMC10 and EMC11 are separated terrestrially by steep embankments and a road but are connected aquatically by an 18 inch culvert pipe.

To determine the extent of spatial resource overlap between red-bellied turtles and red-eared slider turtles I examined habitat use of both species at SLNC and FM using intensive trapping and radio telemetry.

Intensive Trapping

Intensive trapping included the use of baited hoop traps, basking traps and opportunistic hand captures. I baited hoop traps with whole kernel corn and punctured cans of sardines in water or oil. Trapping resulted in captures of eastern painted turtles (*Chrysemys picta*), American snapping turtle (*Chelydra serpentina*), red-bellied turtles (*Pseudemys rubriventris*), stinkpot turtles (*Sternotherus odoratus*) and red-eared slider turtles (*Trachemys scripta elegans*), however all analyses focus strictly on red-bellied turtles and red-eared slider turtles. I recorded UTM locations of each capture with hand held Garmin GPS units. I trapped turtles at SLNC in 2006, 2008, 2009 and 2010 and at FM in 2008, 2009 and 2010. For each turtle captured I determined the species and sex, I estimated age if possible from plastron annuli and recorded the carapace length, carapace height, carapace width, plastron length and mass. In addition I recorded any shell

abnormalities, injuries and apparent health. I marked all turtles with marginal notch codes. Once processed, turtles were released near the site of capture. Trapping effort at each site was calculated by taking the sum of the number of traps set at each wetland per year and the number of days that traps were set.

$$\text{equation 1. Trapping Effort} = \left(\sum \text{Trap \#} * \sum \text{Trap days} \right)$$

Trapping results allowed us to determine relative abundance and densities for both red-bellied turtles and red-eared slider turtles in relation to the entire turtle community. I calculated relative abundance as the percentage of individuals captured of a given species in relation to the total number of individuals from all species that were captured. An entire turtle community of a single species would make up a relative abundance of 1.

$$\text{equation 2. Percent Relative Abundance} = \frac{\# \text{ of individuals per species}}{\text{Total \# of individual turtles}} * 100$$

Abundance Estimates

Using the capture data and encounter histories for each individual turtle I estimated population sizes for red-bellied turtles and red-eared slider turtles at the Silver Lake Nature Center (SLNC) wetland complex and the Fort Mifflin wetland complex (FM).

For red-bellied turtles I used the Cormack-Jolly-Seber (CJS) open population model. I used that model because I had mark-recapture data collected over more than three years and within wetlands that probably did not have emigration or immigration rates of zero. When using the CJS model to estimate populations size the following four

assumptions are made 1. There is equal probability of catching marked or unmarked individuals, 2. The probability of survival between sampling periods is equal for all individuals, 3. Marks are permanent and not overlooked upon capture and 4. Sampling periods are short compared to time periods between sampling (Krebs 1999). I believe that all four of these assumptions were met within my study sites. Population estimates were made in Program MARK using the POPAN program (White and Burnham 1999). I compared CJS models that maintained stable survivorship and catchability rates or varied these parameters in time. I used Akaike Information Criteria (AIC) to determine the best model estimation of population size. If AIC values were close to one another I used the model that maintained equal survivorship and catchability as parameters in the final population estimate.

For red-eared slider turtles which were removed in three out of four years at SLNC and two out of three years at FM I used the catch-effort methods originally described by Leslie and Davis (1939) with the Ricker modification (Krebs 1989). This method relies on linear regression to estimate population size by regressing the catch per unit effort on the cumulative catch. The assumptions used in this model are: 1. That the population is closed, 2. There is equal probability of catching individuals throughout the experiment and 3. All individuals have the same probability of being caught (Krebs 1989). It is likely that the first assumption is violated but that the second and third assumptions were not violated. The assumption that I sampled from a closed population is likely violated because I trapped and removed turtles over several years; a period of time in which there were likely turtles introduced to the population through immigration and pet releases and turtles may have also emigrated from the study site. Immigration to

the population will lead to positively biased estimates while emigrations leads to negatively biased estimations (Bryant 2000, Williams et al. 2002). I am not certain whether immigration or emigration is greater for introduced red-eared slider turtles and assume that these estimates are reliable estimates of the red-eared slider turtle population at the start of my studies.

In addition to estimating the population of each species I also estimated the density of each species within SLNC and FM. Estimates were made by dividing the CJS population estimates by the area of the wetland complex.

$$\text{equation 3. Turtle Density} = \frac{\text{Population Estimate}}{\text{Area of wetland Complex}}$$

I determined the area of each wetland complex using ArcGIS 9.3 by digitizing aquatic habitat boundaries using aerial photographs. Digitized boundaries were converted into polygons and area was calculated using Hawth's Tools (Beyer 2004, Steiniger and Hay 2009). I summed the total area of individual wetlands within a complex to calculate the total amount of aquatic habitat available for turtles to use within a wetland complex.

Radio telemetry

I tracked turtles fitted with radio transmitters at SLNC in 2006, 2008 and 2009 and at FM in 2008 and 2009. I used transmitters with an expected battery life of 9-12 months which provided us the opportunity to track turtles in two different years. In 2006 I used Hollowill transmitters (model AI2, 17g) and AVM (model G3, 12 g) transmitters. In 2008 I used refurbished AVM (model G3, 12g) transmitters and SirTrack transmitters (model HVG154, 14 g) and in 2009 I used SirTrack transmitters only. Turtles were

tracked either by homing or with triangulation. I attempted to locate each turtle at least on a weekly basis.

At SLNC I tracked 12 (6m,6f) red-bellied turtles in 2006, 11 (5m,6f) red-bellied turtles and 7 (2m,5F) red-eared slider turtles in 2008 and 10 (5m, 5f) red-bellied turtles and 7(2M, 5F) red-eared slider turtles in 2009.

At FM I tracked 10 (6m, 4f) red-bellied turtles and 7 (2m,5f) red-eared slider turtles in 2009 and 6 (3m,3f) red-bellied turtles and 1(1m,0f)red-eared slider turtles in 2010 (Table 1).

Within Wetland Species Distributions and Habitat Use

I plotted each data point from both trapping and telemetry data for red-bellied turtles and red-eared slider turtles on background maps of my study sites in ESRI ArcGIS 10.0 software to determine if there were differences in the distributions of each species. Visual inference was used to determine if the two species used macro-habitat of a wetland complex differently. The data were not examined to determine the microhabitat habitat use for individual turtles or for a species.

Results

I captured 270 individual red-bellied turtles and 175 individual red-eared slider turtles at Silver Lake Nature Center and 81 individual red-bellied turtles and 51 individual red-eared slider turtles at Fort Mifflin between 2006 and 2011 during 5585 trap days using baited hoop traps and basking traps (Table 1).

Relative Abundance

At Fort Mifflin the overall relative abundance of red-bellied turtles was 9% of all individual turtle captures while red-eared slider turtles were 6% of all individual turtle captures. At the Silver Lake Nature center red-bellied turtles were 14% of all individual turtle captures and red-eared slider turtles were 9% of all individual turtle captures.

At Fort Mifflin in 2008 the relative abundance of red-eared slider turtles and red-bellied turtles were the same in the moat. In 2009 the relative abundance of red-bellied turtles was higher than that of red-eared slider turtles in the moat but the same in EMC10. I removed red-eared slider turtles from Fort Mifflin in 2009 and 2010. In 2010 Red-bellied turtle relative abundance was greater in both the moat and EMC10 (Table 4).

At Silver Lake Nature Center in 2006 red-bellied turtles had higher relative abundances in Silver Lake and Mill Creek but not in Magnolia Lake (Table 4). All red-eared slider turtles were removed in 2006. When I next trapped in 2008 the relative abundances in Magnolia Lake and Mill Creek were roughly equal between species and red-bellied turtle relative abundance remained higher in Silver Lake (Table 4). In 2009 red-bellied turtles had higher relative abundances than red-eared slider turtles in all of the wetlands. (Table 4). I removed red-eared slider turtles in 2009 and in 2010 the relative abundances of red-bellied turtles remained higher than that of red-eared slider turtles. These data indicate that relative abundances may vary yearly within wetlands, most probably due to unbalanced movements into and out of these wetlands by migrating turtles. My removal of red-eared slider turtles during the course of the study also impacted the relative abundances of both species.

Population Estimates and Species Density Estimates

Trapping data and wetland size were used to estimate population sizes and species specific densities at the Silver Lake Nature Center (SLNC) and at Fort Mifflin (FM) (Table 5). At FM, the red-bellied turtle population was estimated to be 284 with a 95% CI of 210 – 415 turtles and the density to be 71 turtles per hectare. Red-eared slider turtle population was estimated to be 96 with a 95% CI of 52 – 1030 and the density to be 24 turtles per hectare. At SLNC the red-bellied turtle population was estimated to be 764 with a 95% CI of 619 – 973 and the density to be 36 turtles per hectare. The red-eared slider turtle population was estimated to be 216 with a 95% CI of 118 – 313 and the density to be 10 turtles per hectare.

Species Distributions and Habitat Use within Wetlands

Tracking resulted in spatial data for turtles ranging between 3 locations and 37 locations for an individual turtle. A summary of radio tracked individuals can be found in Table 6 and individual turtle locations can be found in appendices 2-5. Combined trapping data and telemetry data show that at both Fort Mifflin and the Silver Lake Nature Center red-bellied turtles and red-eared slider turtles use the wetlands ubiquitously (Figure 1,2). At both sites I have more re-location data for red-bellied turtles which increases the overall coverage by red-bellied turtles. However, red-eared slider turtles were also trapped and tracked throughout each wetland complex.

Discussion

Red-bellied turtles and red-eared slider turtles utilized the same habitat within two wetland complexes. The most basic criteria for two species to compete with one another is that they co-exist in space. Two species that do not coexist in the same locations

cannot use the same resources and cannot affect one another's growth, fecundity or survivorship. My results support the hypothesis that both red-bellied turtles and red-eared slider turtles utilize the same space at Silver lake Nature Center and at Fort Mifflin. Both of these wetland complexes are relatively small in comparison to large lakes or rivers that they could also co-inhabit. Adult red-eared slider turtles have home ranges greater than 15 hectares (Schubauer et al. 1990). Home ranges of *Pseudemys rubriventris* have not been published but other species from the genus *Pseudemys* have had their spatial habitats examined. In *Pseudemys nelsoni* and *Pseudemys floridina* adult turtles were shown to travel over 900 m linear distance (Kramer 1995) while *Pseudemys cocinna* were shown to travel as far as 2.3 km linear distance (Kornilev et al. 2010). None of the wetlands studied at Silver Lake Nature Center or Fort Mifflin are greater in size than the 15 or more hectares of area that red-eared slider turtles might use or longer in linear distance than those traversed by other closely related *Pseudemys* species. Species that exist in the same locations potentially can impact the fitness of one another. How red-eared slider turtles and red-bellied turtles interact in shared habitats will define the potential sources and extent of competition between these two species. If these species simply coexist in the same habitat but are not ecologically similar then I predict that these species would have little impact on one another. However, if these species are ecologically similar they may competitively interact with one another by limiting access to resources such as food, basking sites or nesting sites. Literature on these two species suggest that they are ecologically similar and that if they are sympatric within a wetland complex that they likely would interact for resources (Ernst et al. 1994, Stone 2010).

Important to resource competition are the relative abundance and density of individuals utilizing a resource along with the amount of resource available. In terms of relative abundance the results from intensive trapping shows that the relative abundance of red-eared slider turtles can be quite high in some wetlands (e.g. Magnolia Lake, 2006, Table 4). Furthermore, relative abundance data from SLNC and FM suggest that at the start of my studies within each wetland complex the relative abundance of red-eared slider turtles and red-bellied turtles were similar to one another (i.e. 0.11 at SLNC, 2006 and 0.06 at FM, 2008 Table 3) but after removing red-eared slider turtles the relative abundance of red-eared slider turtles decreased to 0.05 in both SLNC and FM and the relative abundance of red-bellied turtles increased at SLNC to 0.12 and 0.08 at FM by 2010 (Table 3). Red-eared slider relative abundance may have also decreased due to other causes such as a high mortality event or high emigration rates from the study sites. The increased relative abundance of red-bellied turtles may not have been solely due to reduced red-eared slider numbers but may have been due to high immigration to the study sites or increased recruitment. Furthermore, in the greater Fort Mifflin area 57 red-eared slider turtles were removed between 2005 and 2006 during a study of the wetlands in and around the Philadelphia International Airport (Avery et al. 2006). Had these removals not occurred the relative abundance of red-eared slider turtles would have been even higher at Fort Mifflin during this study.

Regardless of the cause for the decrease in relative abundance and population size of red-eared slider turtles over the time period of our study, the decreased relative abundance and population size are likely a temporary setback in population growth. Red-eared slider turtles successfully reproduce across the region and adult red-eared slider

turtles continue to be introduced throughout the region by escaped or released pets. Considering that I worked in two wetland complexes that are both easily accessible by human populations to release pet turtles the population size of red-eared slider turtles across the region may be quite large.

Conservation Implications

Red-eared slider turtles are found living in sympatry with red-bellied turtles and other native species in southeastern PA wetlands. It is likely that these species interact for spatially distributed resources such as food or basking sites within their shared environments. Both red-eared slider turtles and red-bellied turtles are found ubiquitously throughout the wetland complexes that I studied. If these species utilize the same dietary, nesting or thermoregulatory habitat they may potentially compete for those resources if they are or become limiting. It is likely that in some habitats where both red-bellied turtles and red-eared slider turtles are living that resource limitations occur seasonally if not constantly. Competition between species can have long term impacts on the growth, reproduction and survivorship of either species.

To further prevent the continued growth of red-eared slider turtle populations the continued introduction of pet turtles to wetlands should be prevented through a ban on non-native turtles being sold in the pet trade. Furthermore, long-term intensive trapping may be an effective control measure to reduce the abundance of red-eared slider turtles and limit their impact on native species. Without a clear understanding of the long term impacts of red-eared slider turtles on red-bellied turtles and other native species the removal and prohibition of releasing red-eared slider turtles should be continued. If red-eared slider turtles are considered naturalized and no longer managed as an invasive

species, their populations will continue to grow and their ecological impact and damage will grow and may detrimentally impact red-bellied turtle population and other native species.

Table 2-1. Number of individual red-bellied turtles (*Pr*), individual red-eared slider turtles (*Ts*) and individuals from all other species captured at Fort Mifflin (FM) and Silver Lake Nature Center (SLNC) by year. Numbers of individuals for each of the other species are available in appendix B.

Year	Wetland	Species		
		<i>Pr</i>	<i>Ts</i>	Other species
2006	SLNC	52	51	357
2008	SLNC	159	87	756
	FM	17	15	236
2009	SLNC	46	14	212
	FM	75	28	574
2010	SLNC	57	23	411
	FM	27	17	307
2011	SLNC	4	2	46

Table 2-2. Percent relative abundance of individual red-bellied turtles (*Pr*), individual red-eared slider turtles (*Ts*) and individuals from all other species captured at Fort Mifflin (FM) and at Silver Lake Nature Center (SLNC) between 2006 and 2011. Relative abundances for each of the other species are available in appendix D.

Year	Wetland	Relative Abundance % of individuals captured		
		<i>Pr</i>	<i>Ts</i>	Other species
2006	SLNC	11	11	78
2008	SLNC	16	9	75
	FM	6	6	88
2009	SLNC	17	5	79
	FM	11	4	85
2010	SLNC	12	5	83
	FM	8	5	87
2011	SLNC	8	4	88

Table 2-3. Percent relative abundance of red-bellied turtles (*Pr*) and red-eared slider turtles (*Ts*) in the individual wetlands at Fort Mifflin (FM) and Silver Lake Nature Center (SLNC) individual wetlands between 2006 and 2011. Relative abundance for each of the other species are available in the appendices.

Year	Wetland Complex	Wetland Name	Relative Abundance % of individuals captured		
			<i>Pr</i>	<i>Ts</i>	Other species
2006	SLNC	Magnolia Lake	4	17	79
		Mill Creek	14	3	83
		Silver Lake	13	3	84
2008	FM	Moat	6	6	88
	SLNC	Magnolia Lake	14	13	77
		Mill Creek	5	5	90
		N. Mill Creek	0	1	99
		Silver Lake	2	5	93
		Unconnected Pond	0	25	75
2009	FM	Delaware River	0	0	100
		EMC-10	1	1	98
		EMC-11	0	0	100
		Moat	13	2	85
	SLNC	Magnolia Lake	17	4	79
		Mill Creek	1	5	94
		Silver Lake	1	4	95
		Unconnected Pond	8	8	84
2010	FM	EMC-10	8	4	88
		Moat	5	4	91
	SLNC	Magnolia Lake	9	4	87
		Mill Creek	9	3	88
		Silver Lake	11	4	85
2011	SLNC	Silver Lake	6	3	91

Table 2-4. Population estimates and density for red-bellied turtles (*P. rubriventris*) using Cormack-Jolly-Seber open model population estimates and population estimates and density for red-eared slider turtles (*T. scripta*) using the Leslie method of removal estimates at Fort Mifflin and at Silver Lake Nature Center.

Wetland	Species	Population Estimate	Standard Error	Low Estimate	High Estimate	Species Density/ Ha
Fort Mifflin	<i>P. rubriventris</i>	284	50.7	210	415	71
	<i>T. scripta</i>	96	73.5	52	1030	24
Silver Lake Nature Center	<i>P. rubriventris</i>	764	89	619	973	36
	<i>T. scripta</i>	216	22.6	118	313	10

Table 2-5. Summary of individual turtles that were radio-tracked at Silver Lake Nature Center (SLNC) in 2006, 2008, 2009 and at Fort Mifflin (FM) in 2009 and 2010.

Year	Wetland	Species	Males	Females	Total
2006	SLNC	<i>Pr</i>	6	6	12
		<i>Ts</i>	0	0	0
2008	SLNC	<i>Pr</i>	5	6	11
		<i>Ts</i>	2	5	7
2009	SLNC	<i>Pr</i>	5	5	10
		<i>Ts</i>	2	5	7
	FM	<i>Pr</i>	6	4	10
		<i>Ts</i>	2	5	7
2010	FM	<i>Pr</i>	3	3	6
		<i>Ts</i>	1	0	1

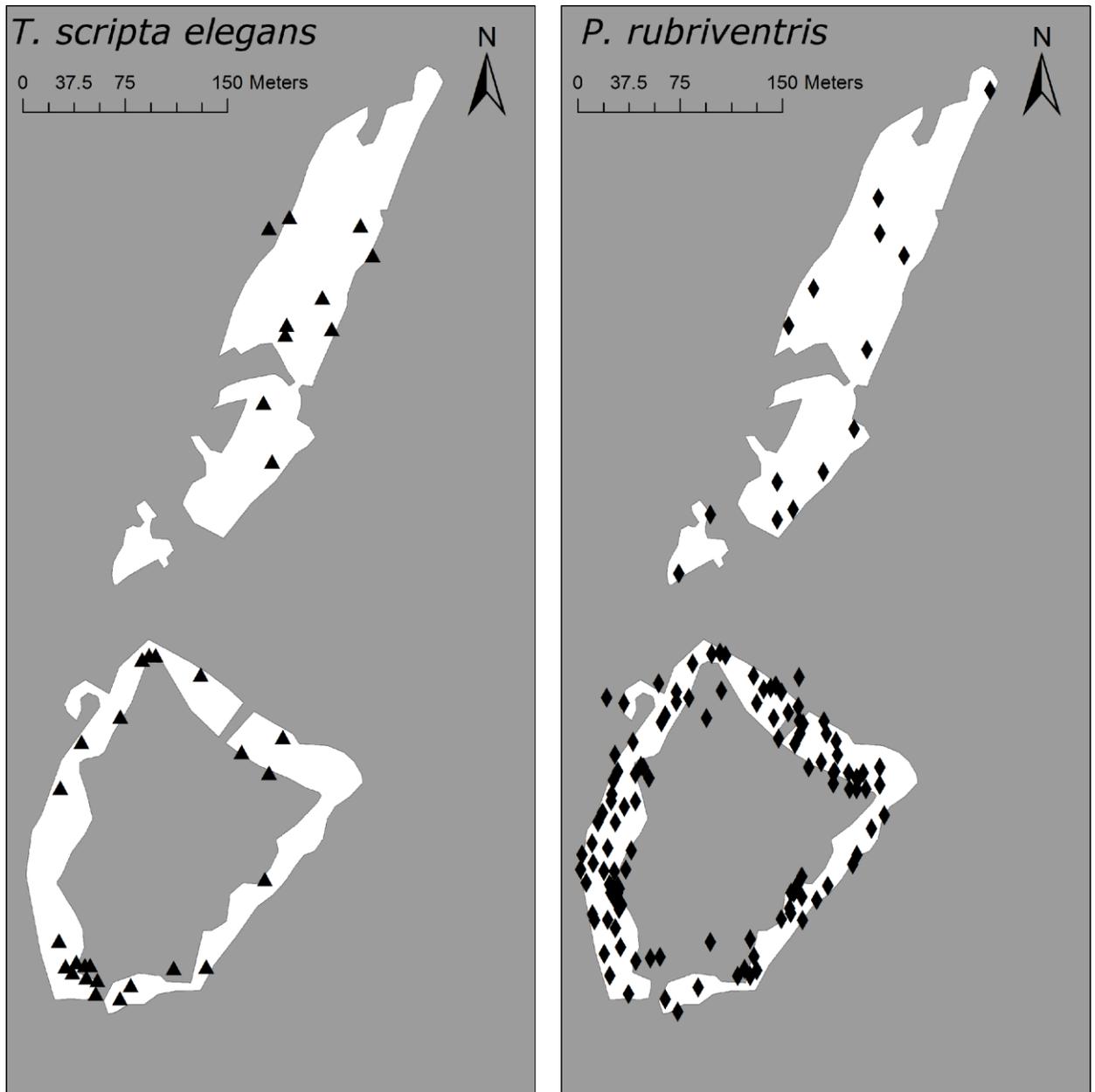


Figure 2-1. General habitat use by red-bellied turtles (*P. rubriventris*) and red-eared slider turtles (*T. scripta elegans*) at Fort Mifflin. Data presented are all trapping and radio telemetry relocations at FM between 2008 and 2010.

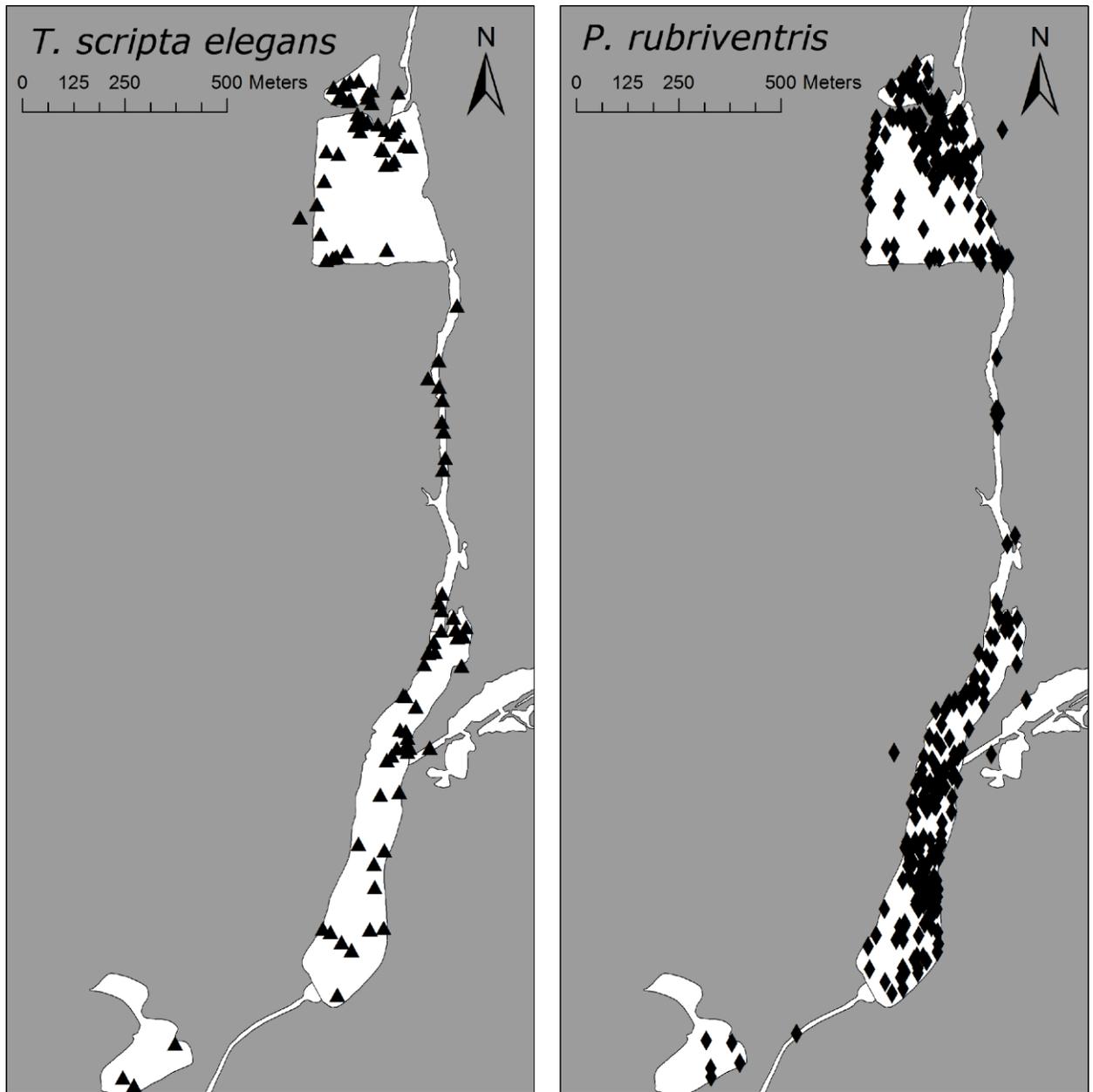
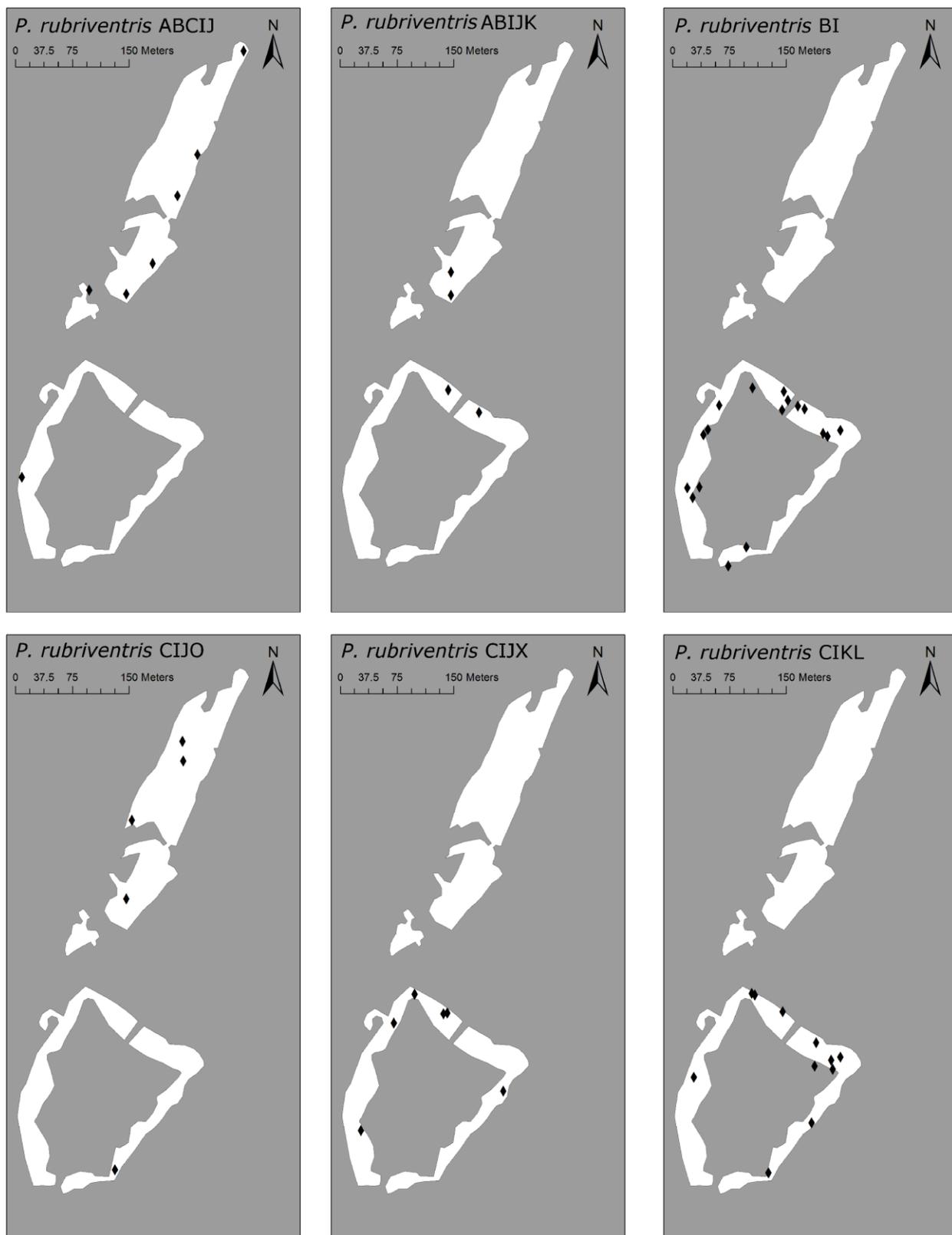


Figure 2-2. General habitat use by red-bellied turtles (*P. rubriventris*) and red-eared slider turtles (*T. scripta elegans*) at Silver Lake Nature Center (SLNC). Data presented are all trapping and radio telemetry relocations at SLNC between 2006 and 2010.

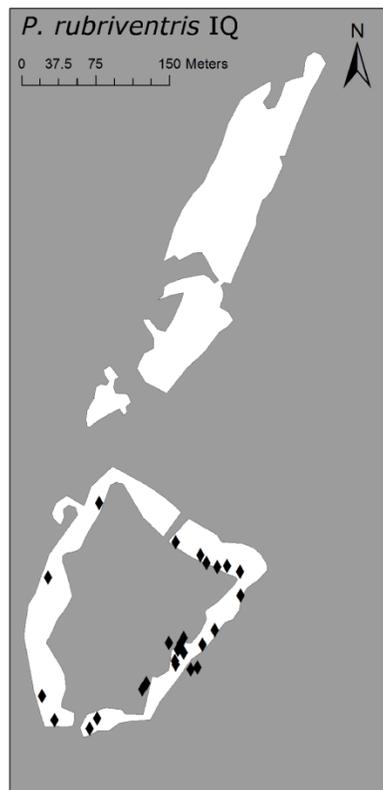
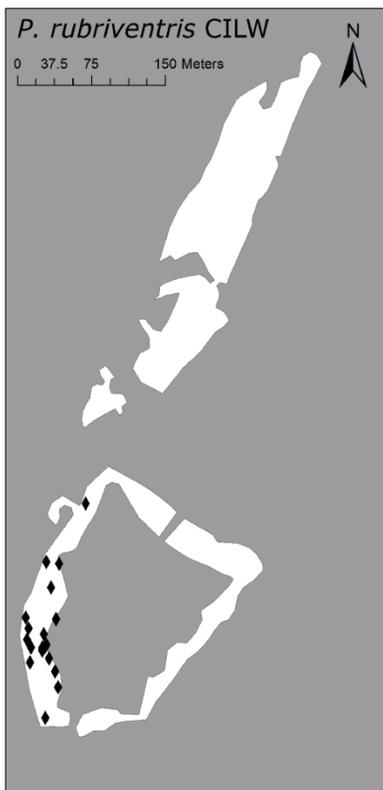
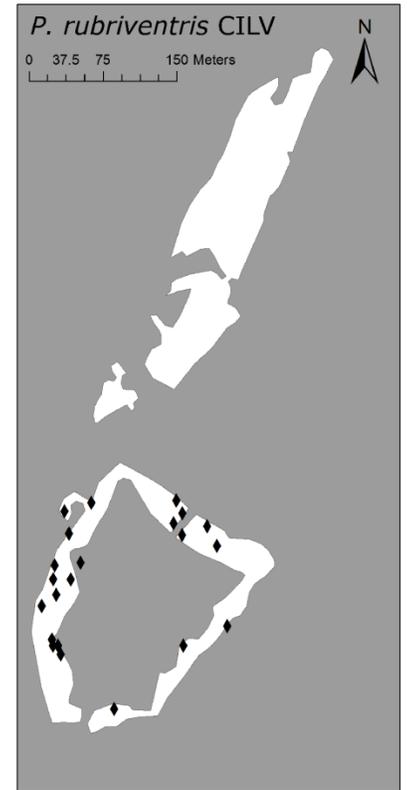
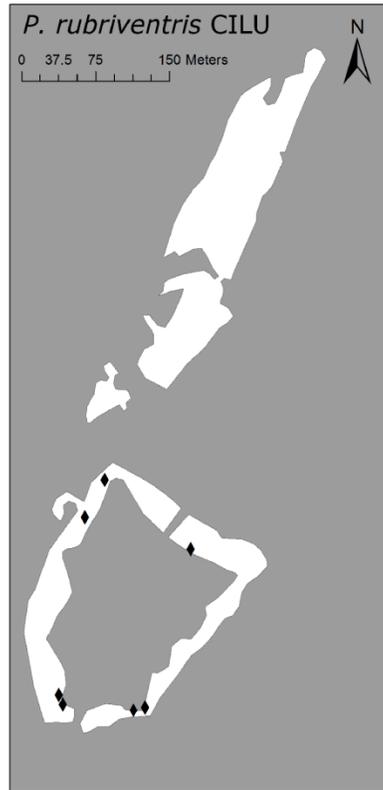
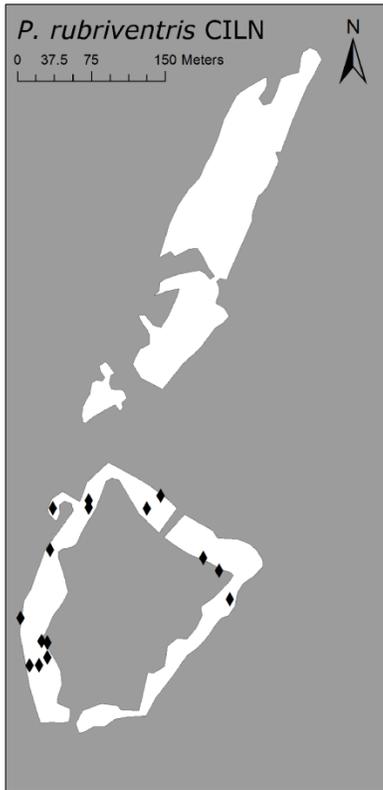
Appendices

Appendix 1. Trapping effort in individual wetlands expressed in number of days spent trapping.

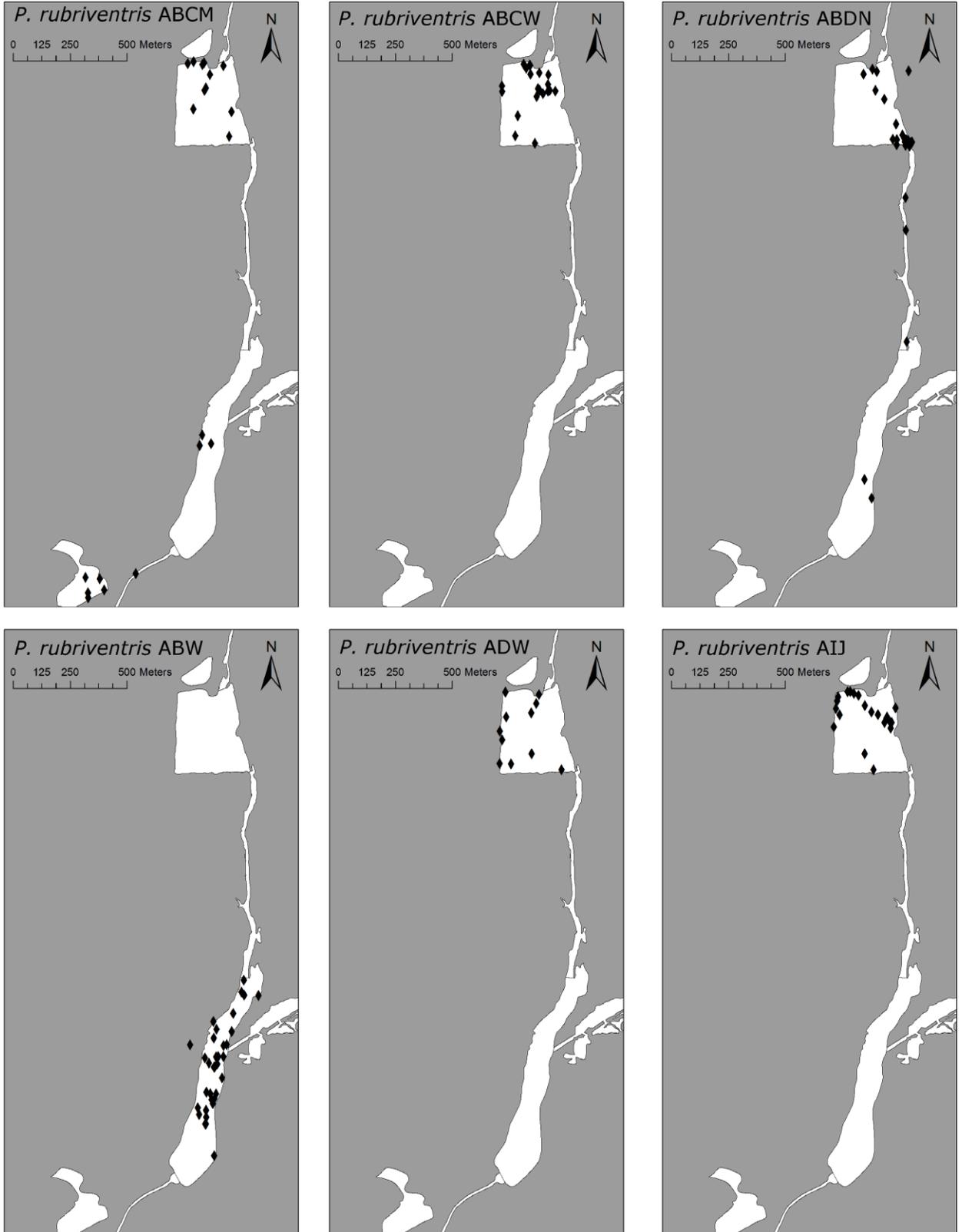
	Wetland Complex	Wetland Name	Wetland Type	Trap Effort Baited	Trap Effort Basking	Trap Effort Total
2006	SLNC	Silver Lake	Lake	247	0	247
		Mill Creek	Creek	82	0	82
		Magnolia Lake	Lake	238	0	238
		Unconnected Pond	Lake	10	0	10
2008	FM	Moat	Lake	240	0	240
		Delaware River	River	44	129	173
	SLNC	Silver Lake	Lake	810	46	856
		Mill Creek	Creek	524	46	570
		Magnolia Lake	Lake	506	36	542
2009	FM	Moat	Lake	423	0	423
		EMC-10	Lake	210	0	210
		EMC-11	Lake	8	0	8
	SLNC	Silver Lake	Lake	116	0	116
		Mill Creek	Creek	40	0	40
		Magnolia Lake	Lake	162	161	323
		Unconnected Pond	Lake	9	0	9
2010	FM	Moat	Lake	173	0	173
		EMC-10	Lake	258	0	258
	SLNC	Silver Lake	Lake	260	1	261
		Mill Creek	Creek	61	0	61
		Magnolia Lake	Lake	289	0	289
2011	SLNC	Silver Lake	Lake	60	0	60
		Mill Creek	Creek	1	0	1

Appendix 2. Maps of individual turtle locations for red-bellied turtles at Fort Mifflin

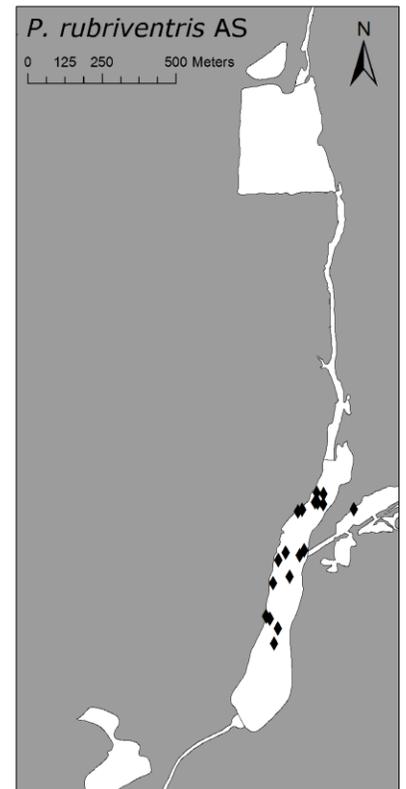
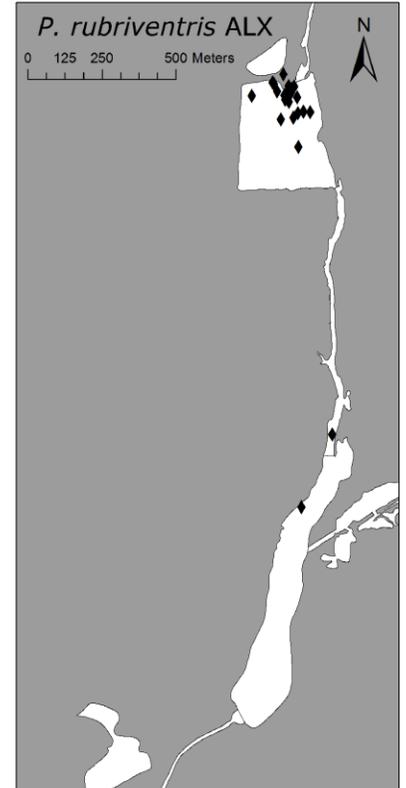
Appendix 2 continued.



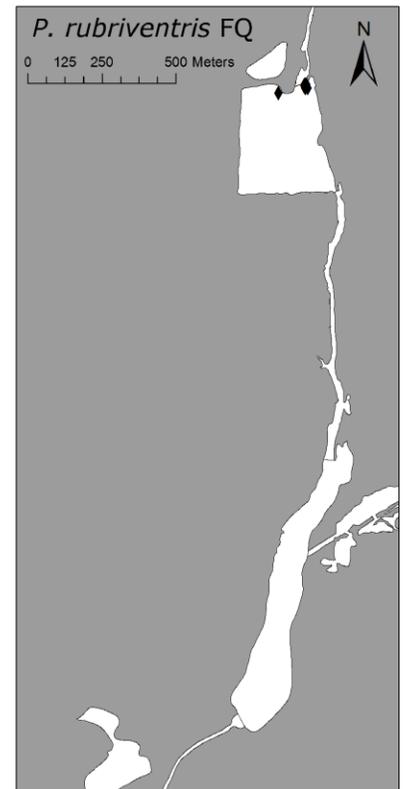
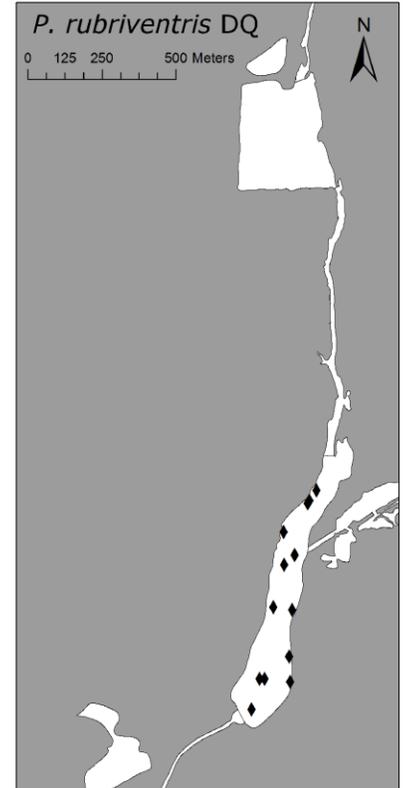
Appendix 3. Maps of individual turtle locations for red-eared slider turtles at FM

Appendix 4. Maps of individual turtle locations for red-bellied turtles at SLNC

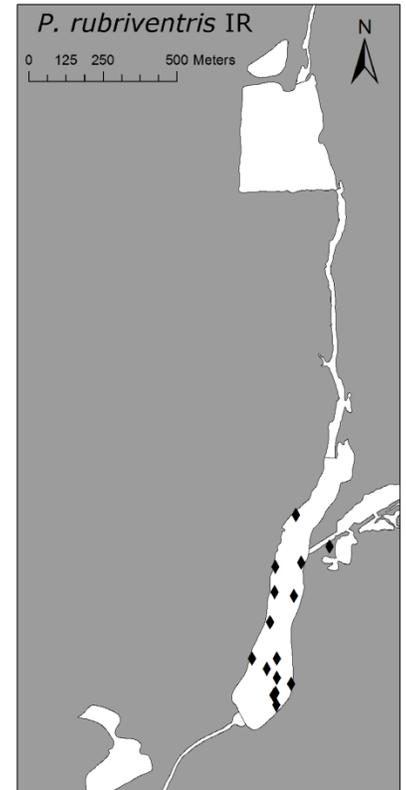
Appendix 4 continued



Appendix 4 continued



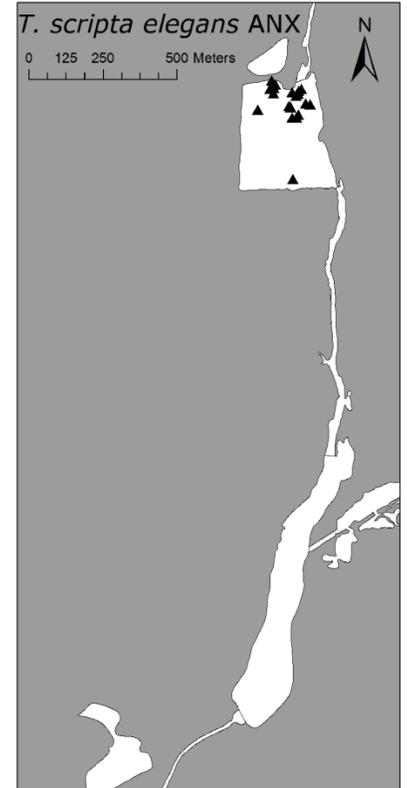
Appendix 4 continued



Appendix 5. Maps of individual locations for red-eared slider turtles at SLNC



Appendix 5 continued.



CHAPTER 3: Stable isotopes of C and N reveal habitat dependent dietary overlap between native and introduced turtles *Pseudemys rubriventris* and *Trachemys scripta* (PLoS ONE 8(5), 2013)

Abstract

Habitat degradation and species introductions are two of the leading causes of species declines on a global scale. Invasive species negatively impact native species through predation and competition for limited resources. The impacts of invasive species may be increased in habitats where habitat degradation is higher due to reductions of prey abundance and distribution. Using stable isotope analyses and extensive measurements of resource availability we determined how resource availability impacts the long term carbon and nitrogen assimilation of the invasive red-eared slider turtle (*Trachemys scripta elegans*) and a native, threatened species, the red-bellied turtle (*Pseudemys rubriventris*) at two different freshwater wetland complexes in Pennsylvania, USA. At a larger wetland complex with greater vegetative species richness and diversity, our stable isotope analyses showed dietary niche partitioning between species, whereas analyses from a smaller wetland complex with lower vegetative species richness and diversity showed significant dietary niche overlap. Determining the potential for competition between these two turtle species is important to understanding the ecological impacts of red-eared slider turtles in wetland habitats. In smaller wetlands with increased potential for competition between native turtles and invasive red-eared slider turtles we expect that when shared resources become limited, red-eared slider turtles will negatively impact native turtle species leading to long term population declines. Protection of intact

wetland complexes and the reduction of introduced species populations are paramount to preserving populations of native species.

Introduction

Habitat degradation is the leading cause of extinction and population declines worldwide (Wilcove et al. 1998). Species richness and species diversity generally decrease as habitat availability is reduced and rates of disturbance increase (Fahrig 2003, Shenko et al. 2012). For species in the same guild of an ecological community, decreases in resource availability can lead to increases in resource overlap and a narrowing of niche breadth (Swihart et al. 2003b, Luiselli 2006) leading to increased risk of resource competition (Bellgrah et al. 2008). Competition for shared resources between species often negatively impacts the growth rates, fecundity rates and/or survivorship of at least one of the competing species (Polis and McCormick 1987). Disturbed habitats are susceptible to the establishment of introduced species due to alteration of community structure with open niches that can be filled by non-native species (D'Antonio and Vitousek 1992, Mack et al. 2000a).

Today, naturally evolved and established ecological communities are being disrupted at unprecedented rates through habitat degradation and species introductions (Wilcove et al. 1998), leading to alterations in resource availability and changes in community structure (Fahrig 2003). Native species are negatively impacted by introduced species through predation and competition (Alison et al. 1995). Introduced predators can cause the severe collapse of native faunas that do not adapt quickly enough to increased predation rates (Sibly and Atkinson 1994, Rodda et al. 1997). Introduced

competitors cause decline of native species by increasing rates of exploitative and interference competition (Polis and McCormick 1987, Amarasekare 2002). When competition occurs for limited resources the species that more efficiently utilizes resources will competitively exclude the less efficient species (Tilman 1981, Cadotte 2007). Co-existence between competing species can occur if inferior competitors disperse more rapidly or utilize resources that shift in space and time (Amarasekare et al. 2004). Competition between species may result when dietary resources are not partitioned and will cause reduced fitness levels of one or all competing species (Polis and McCormick 1987).

Ecological studies of diets have historically relied on short term dietary intake through observations of feeding and/or the collection of stomach contents through fecal collection, stomach flushing or dissection (Hansen 1976, Rowe 1992, Paoletti and Puig 2007). Long term diets of organisms have been studied through the analyses of carbon 13 and nitrogen 15 stable isotopic fractions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) (Peterson and Fry 1987, Reich et al. 2007, Wallace et al. 2009). Naturally occurring isotopic fractions of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) indicate an organism's trophic level and the source of carbon assimilated from its diet, respectively (Post 2002). The premise of all stable isotope studies of animals is that isotopes of the same element are incorporated at different rates into tissue through nutrient assimilation by an organism during digestion or other physiological processes (Fry 2006, Kilham et al. 2009). Factors affecting $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope assimilation include tissue metabolism, trophic level, temperature, C:N ratios in items consumed, taxonomy, body size, and an organism's form of eliminating

nitrogenous waste (Vanderklift and Ponsard 2003, Kilham et al. 2009). Stable isotopes have been used in determining the C and N sources in organisms' diets (Bulte and Blouin-Demers 2008), trophic position in food webs (Bluthgen et al. 2003) and in comparative studies of species feeding ecology between study sites (Kemp 2008, Alves-Stanley et al. 2010, Miranda and Perissinotto 2012).

We used stable isotope analyses to quantify the diets and extent of resource overlap between the native red-bellied turtle (*Pseudemys rubriventris*) and the introduced red-eared slider turtle (*Trachemys scripta elegans*) in two southeastern Pennsylvania wetland complexes that differed in ecological characteristics. Red-eared slider turtles have been introduced globally and negatively impact basking behavior and growth rates of European pond turtles (*Emys orbicularis galloitalica*) and the Spanish terrapin (*Mauremys leprosa*) under experimental and natural conditions (Cadi and Joly 2004, Polo-Cavia et al. 2009a). We relate the results of stable isotope analyses to wetland characteristics and the potential for competition between red-bellied turtles and red-eared slider turtles.

Study Sites

We carried out our research at two wetland complexes that differed in size, extent of connectivity, and the species richness and diversity of vegetative communities. One wetland complex was located at the Silver Lake Nature Center (SLNC), Bristol, PA and consisted of two lakes each greater than nine hectares which were connected by a creek and surrounded by protected lowland forest and parkland. The second wetland complex was at Fort Mifflin (FM), Philadelphia, PA and consisted of three small wetlands, each

less than 0.8 hectares separated by steep banks and paved roads, and surrounded by mowed lawns and narrow patches of forest (Table 1).

Materials and Methods

Ethics Statement

We collected all animals and tissue samples under the Drexel University Institutional Animal Care and Use Committee approved protocol # 18487 and Pennsylvania Fish and Boat Commission Scientific Collecting Permits # 121 issued to HWA and #345 issued to SHP. Permission to collect at SLNC and FM was granted by the land managers.

Calculation of Wetland Size

We calculated wetland size using ArcGIS 9.3 by digitizing aquatic habitat boundaries using aerial photographs. Digitized boundaries were converted into polygons and area was calculated using Hawth's Tools (Beyer 2004, Steiniger and Hay 2009). We summed the total area of individual wetlands to calculate the total amount of aquatic habitat available for turtles to use within study sites.

Availability of Vegetation Resources

We determined vegetative community composition through monthly vegetation surveys performed between June and September 2010. We used a hybridized quadrat-belt transect sampling technique (Titus 1993). At each wetland within a wetland complex we chose 10 littoral zone transect sites by randomly selecting 10 points along the wetland's perimeter using ArcGIS software. We located survey points using handheld

Garmin GPS units and then determined final location randomly (Seastedt et al. 1991, Ervin 2007). Each transect was 3 m long and ran perpendicular to the wetland edge. Along each transect, three 0.5 m² quadrats were sampled with 1.5 m center spacing. This sampling technique enabled determination of species composition in each quadrat and an estimate of percent cover for terrestrial plants and submerged, emergent and floating macrophytes across a 3 m gradient of water depth. We used these data to determine species richness and species diversity of riparian vegetation at each wetland studied. Species diversity was determined using the Shannon Wiener Diversity Index in which H' is the diversity

$$H' = \sum_{i=1}^S (P_i)(\log_2 P_i)$$

index, s = the number of species and P_i = the proportion of total samples belonging to the i^{th} species (Krebs 1999).

Sampling for Stable Isotopes

Sample Collection -Turtles

We captured turtles by hand, basking traps and baited hoop net traps and took tissue samples from individual sexually mature adult turtles during the active season (June through September) over a three year period (2008,2009,2010). Red-eared slider turtles are sexually dimorphic so we sampled sexually mature male red-eared slider turtles greater than 100 mm straight plastron length (SPL) and females greater than 175 mm SPL (Gibbons and Greene 1990, Ernst et al. 1994). Red-bellied turtles exhibit less

pronounced sexual dimorphism so all turtles sampled were greater than 175 mm SPL (Graham 1971, Ernst et al. 1994). Tissues included blood drawn from the forelimb (Avery and Vitt 1984), tail tissue from the posterior most 3 mm of the turtle's tail and shell filings collected during ID code notching. Stable isotope sample sizes are presented in Table 2. We stored blood on ice or in a freezer for up to 12 hours until we separated blood plasma and red-blood cells by centrifugation. We took samples of tail tissue with sterile scalpel blades. Using clean half round files, we produced shell filings and collected them in sealable plastic bags. Carbon and nitrogen stable isotopes of blood tissue for red-eared slider turtles have a turnover rate of 3-6 months (Seminoff et al. 2007) and are representative of short term nutrient assimilation. Shell and tail tissue turnover rates are unknown for adult turtles but we assume that isotopic composition of these tissues represent diet assimilation over many years.

Sample Collection – Plants

We collected each plant species encountered during the monthly vegetative resource availability surveys described above. We also collected vegetation opportunistically throughout the season to ensure that we sampled all of the potential dietary items. Plants analyzed were processed as whole plants, flowers or fruits.

Sample Preparation and Processing

We processed turtle tissues (Table 2) following techniques described by Seminoff *et al.* (Seminoff et al. 2007). All tissues were dried at 60° C for 24 to 48 hours. Vegetation samples (Table 3) were rinsed with water to ensure that animal material was removed and dried at 60° C for 24 hours. We did not extract lipids or mathematically

normalize $\delta^{13}\text{C}$ values because of the relatively low lipid content in the tissues we analyzed. Turtle blood has a low lipid content compared to birds for which lipid extraction of blood has been determined to be unnecessary (Chaikoff and Entenman 1946, Cherel et al. 2005, Bulte and Blouin-Demers 2008). Furthermore, we determined the percent lipid of tail tissue by lipid extraction with dichloromethane to be below the 5% threshold that Post et al. (2007) suggest lipid extraction or mathematical normalization of $\delta^{13}\text{C}$ be performed on (Post et al. 2007). All samples were sealed and stored frozen until prepared for mass spectrometry. We pulverized dried samples into a homogenous powder with an agate mortar and pestle, with a glass stirring rod or with a liquid nitrogen SPEC Certiprep freezer mill. Pulverized samples weighing 0.6 mg to 1 mg for turtle tissues and 1 mg to 1.5 mg for vegetation samples were placed in 3.5 x 5 mm and 5 x 9 mm pressed tin capsules respectively, sealed and analyzed at the Patrick Center for Environmental Research, the Academy of Natural Sciences, Philadelphia, PA, using a Finnigan Delta Plus coupled to a NA2500 Elemental Analyzer (EA-IRMS). Cross contamination was avoided by cleaning all processing equipment before and after each sample. Samples were run in duplicate or triplicate and analytical variability was generally less than 3% RSD. Multiple in-house standards were analyzed for each run to assess comparability over time. Samples were reported in the standard δ (‰) notation:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$$

where X is either ^{13}C or ^{15}N and R is either $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The $\delta^{15}\text{N}$ standard was air ($\delta^{15}\text{N}=0$), and the $\delta^{13}\text{C}$ standard was the Vienna PeeDee Belemnite (VPDB) limestone that was assigned a value of 0.0‰. Analytical accuracy was based on standardization of

scientific grade N₂ and CO₂ used for continuous flow-IRMS with International Atomic Energy Agency's (IAEA) N-1, N-3, and USGS 26 for nitrogen and IAEA's sucrose, National Institute of Standards and Technology's (NIST) NBS 19, and NIST's NBS 22 for carbon, respectively.

Data Analysis

We analyzed results of stable isotope analysis by first averaging $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for individual samples with replicated tissues. Averaged values were then used for all subsequent analyses. We analyzed isotopic values within year and by tissue in R using standard t-tests (unequal variance assumed) with species as the grouping factor. We accepted statistical significance at the $p = 0.05$ level. In this study, a significant difference between species within a year was representative of isotopic niche partitioning. We analyzed isotopic values between years and by tissue using fixed effect ANOVAs with year as the treatment and isotopic means as the response variable with program R (R Development Core Team 2011). All comparisons between years were significantly different and we did not combine data between years. Significant differences between years may not be representative of dietary shifts due to the temporal variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of aquatic vegetation (McCutchan and Lewis 2001).

Results

Wetland Size, Vegetative Species Richness and Vegetative Species Diversity

Aquatic habitat at SLNC was 5.75 times larger than that at FM. Plant species richness at SLNC was 1.26 times greater than at FM and plant species diversity using the

Shannon-Wiener Diversity Index was 1.45 times greater at SLNC (Table 1). After four monthly surveys the cumulative number of species surveyed at FM had leveled off while at SLNC the number of species was still increasing (Figure 1). Species documented at each wetland are presented in Supplementary Table 1.

Stable Isotope Values

At SLNC there were significant differences between species for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for all turtle tissues representing short term and long term diets (Table 2). At FM no significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values existed for turtle tissue that represented short term diets (Plasma/RBC) (Table 2). In 2008 and 2009 there were significant differences in $\delta^{13}\text{C}$ values in turtle tissues that represented long term diets (tail/shell filings), with red-eared slider turtles having significantly higher $\delta^{13}\text{C}$ values in 2008 and significantly lower values in 2009. In 2009 there was a significant difference in $\delta^{15}\text{N}$ values from turtle tissues that represented long term nitrogen assimilation with red-eared slider turtles having significantly higher $\delta^{15}\text{N}$ values (Table 2). At FM $\delta^{13}\text{C}$ values of plant tissue ranged between -28.5‰ and -16.5‰ and $\delta^{15}\text{N}$ values ranged between 1.03‰ and 10.09‰ (Table 3). At SLNC $\delta^{13}\text{C}$ values of plant tissue ranged between -28.24‰ and -19.92‰ and $\delta^{15}\text{N}$ values ranged between 0.20‰ and 11.02‰ (Table 3).

Lipid Values

Percent lipids of tail tissue were found to be low, with a mean of 1.24%, lipid for all samples, n= 6. Red-bellied turtles had a mean of 1.32% and standard deviation of 1.06, n=3, while red-eared slider turtles had a mean percent lipid of 1.15% and a standard

deviation of 0.62, $n=3$. A two-tailed t-test showed no significant difference between species ($p=0.8$).

Discussion

Potential for competition in different wetlands

To our knowledge this is the first study comparing the isotopic niches of native and introduced species at different sites with measured differences in ecological characteristics. At our study sites anthropogenic impacts resulted in different habitat patch sizes. Historically, both of our study sites were either tidal creeks/ floodplains (SLNC) or associated tidal wetlands of the Delaware River (FM). However, anthropogenic activities created impoundments and protected habitat at SLNC while they degraded the wetlands at FM to remnant impounded patches. These anthropogenic impacts may be the driving force behind our findings that at SLNC the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ niches of red-bellied turtles and red-eared slider turtles did not overlap while the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ niches did overlap at FM. In anthropogenic altered habitats, shifts in the $\delta^{15}\text{N}$ niche of sailfin mollies (*Poecilia latipinna*) led to reduced growth rates in the altered habitat (Kemp 2008).

At SLNC the potential for competition for dietary resources was low as the extent of dietary resource overlap was low. The partitioned $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ niches were likely a factor of larger wetland size, greater vegetative species richness and greater vegetative species diversity which enabled a wider niche base for species to partition. Another potential factor impacting the isotopic niches may have been invertebrate species richness

and diversity. We recognize that animal matter is important to turtle diets but red-bellied turtles and red-eared slider turtles are primarily herbivorous and are known to feed on animal matter opportunistically (Parmenter and Avery 1990, Ernst et al. 1994). Higher $\delta^{15}\text{N}$ levels (Figure 2) of red-eared slider turtles at SLNC may have indicated that animal matter was an important driver of the dietary niche partitioning found at SLNC. Fecal sample examination from both species indicated a tenfold increase in the percent volume of animal matter in the diets of red-eared slider turtles compared to red-bellied turtles at SLNC (Pearson, unpublished data). The higher volume of animal matter in red-eared slider turtle diets is reflected by the significantly greater $\delta^{15}\text{N}$ values compared to red-bellied turtles at SLNC (Table 2/ Figure 2, SLNC).

At FM the potential for competition in the short term was greatly increased as the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ niche axes did not significantly differ between species. Whether or not red-bellied turtles are weaker competitors than red-eared slider turtles for limited resources is yet to be determined. However, when a shared dietary resource between red-bellied turtles and red-eared slider turtles becomes limiting, competition will occur and the species better suited to obtain that resource will negatively impact the growth, fecundity or survivorship of the weaker competitor (Polis and McCormick 1987). Our study showed that under certain conditions (i.e. in smaller wetlands) the potential for competition between red-bellied turtles and red-eared slider turtles did exist. If overlap for resources occurs over extended periods of time it is likely that these species will compete for resources and that this competition will have negative impacts on long term population growth of one of the species (Bellgraph et al. 2008).

Differences in Wetland Characteristics

At SLNC stable isotope signatures indicated that red-eared slider turtles and red-bellied turtles did not utilize the same dietary resources on either a short term or long term basis. This was consistent between years for all tissues sampled. The high vegetative species richness enabled these species to partition diets by consuming different plants at SLNC. At FM stable isotope signatures revealed no significant differences between diets of the two turtle species on a short term basis but indicated differences on a long term basis. These differences between wetland complexes can be due to several factors. One explanation could be that the range of available carbon and nitrogen stable isotopes at FM was narrower. However, this was not the case as the breadth of stable isotope values at FM was not collapsed in comparison to SLNC (Table 3). For the same set of plant species the widest breadth of carbon and nitrogen stable isotope values was found for vegetation sampled from FM. A second explanation could be differences in wetland size. Aquatic habitat available at SLNC was 5.75 times the size of aquatic habitat at FM (Table 1). Smaller habitat size reduces space available to forage which can increase the likelihood that two species will consume the same resources. At FM the depressed niche differentiation between species may have been due in part to a reduction in available habitat. A third possibility for differences in long term dietary niche overlap between wetland complexes could have been differences in dietary resources available. Adult red-bellied turtles and red-eared slider turtles are primarily herbivorous but will eat available animal material (Ernst et al. 1994). At FM the overlap for diets was due in part to FM having fewer plant species to partition (Table 1) while at SLNC the red-eared

slider turtles added invertebrates to their diet causing a greater separation in dietary niches between the species.

Our research occurred at two wetland complexes that represented different disturbance histories. We recognize that we did not replicate these studies in other wetlands with similar sizes and ecological characteristics. However, our results are valid as an example of how wetland characteristics can impact the assimilation of an introduced species into native communities with different disturbance histories. This “natural experiment” (Baum and Worm 2009, Shenko et al. 2012) was designed to determine how wetland characteristics relate to dietary niche overlap between red-eared slider turtles and red-bellied turtles. An increase in vegetative species richness, like that seen at SLNC, may enable red-bellied turtles and red-eared slider turtles to partition dietary resources while a narrower resource base, like that seen at FM, may lead to an increase in dietary resource overlap. Our findings are similar to those of Luiselli *et al.* who report that differences in diets of the west African mud turtle (*Pelusios castaneus*) and the west African black turtle (*Pelusios niger*) at a pristine site and an oil-polluted site in the Nigeria Delta are due to a change in dietary resource availability at the disturbed site (Luiselli et al. 2004). Similarly, Kamler *et al.* report that diets of swift foxes (*Vulpes velox*) are altered based on resource availability in continuous and anthropogenically altered prairie habitats (Kamler et al. 2007).

Long-term Carbon and Nitrogen Isotopic Niche Partitioning at FM

Over the three year period of our study, red-bellied turtles and red-eared slider turtles at FM consistently overlapped in short term diets but their long term diets differed

in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. These data suggest that the turtle populations may be highly transient. This is consistent with findings of inter-wetland movement by marked animals from FM (Avery et al. 2006). Since short term $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values overlapped but long term did not, these species were feeding on similar resources while at FM but had different diets while in other wetlands. Due to the small size of these wetlands it is likely that turtles did not reside in these wetlands for their full lifetime. Therefore, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ represent long term net diet assimilated from other habitats. Our study site at FM was adjacent to the Delaware River which may have provided access to a broader watershed for immigrating turtles to find the site or for emigrating turtles to disperse. In addition to the Delaware River acting as a source or sink of turtles for our study site there was a mosaic of remnant wetlands dotting the landscape between our study site and the John Heinz National Wildlife Refuge (Avery et al. 2006). These wetlands may also have acted as a source or sink for turtles to/from our study site.

Alternate explanations are that red-eared slider turtle long term diet assimilation may be representative of a history of living in captivity or different responses to high protein ephemeral resources. If the red-eared slider turtles that we sampled were released pets we would expect their long term stable isotope signatures to reflect the higher protein signature of domestic turtle food or human food rather than that of wild turtle populations. If red-eared slider turtles respond more rapidly to ephemeral protein sources such as carrion or fluxes of insect larvae their long term isotopic signatures would also reflect a higher protein diet. As seen in Table 2 the nitrogen signature for tail tissue of

red-eared slider turtles was higher than those for red-bellied turtles indicating greater rates of protein consumption by these turtles.

Conservation Implications

The potential for competition between species can increase as anthropogenic impacts become more severe (Swihart et al. 2003b, Luiselli 2006, Bellgraph et al. 2008). When competition occurs between species the negative impacts are not immediate (Schoener 1983) and in long lived species, such as turtles, would likely result in reduced growth rates and decreased body condition (Cadi and Joly 2004). Shifts in growth rates and body condition of turtles can lead to delayed maturity and decreased lifetime fecundity (Congdon and Gibbons 1985, Avery et al. 1993, Litzgus et al. 2008), in turn negatively affecting population size and growth (Congdon et al. 1993, Heppell 1998). If red-eared slider turtles negatively impact red-bellied turtles in Pennsylvania or native species elsewhere, then their introduction may have long term consequences on the structure of turtle communities worldwide. The continued introduction of red-eared slider turtles may lead to decreased population size or extirpation of native turtle species. As a cautionary measure the sale and release of red-eared slider turtles should be prohibited outside their native range while pre-existing owners should be required to register existing pets to further reduce the number of released animals. If continued introductions of red-eared slider turtles are prevented, then targeted control programs may be successful at stemming this species continued invasion.

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Table 3-1. Wetland characteristics at the Silver Lake Nature Center (SLNC) and Fort Mifflin (FM), Pennsylvania, USA. Species richness and diversity of vegetation was greater at Silver Lake Nature Center than at Fort Mifflin.

Wetland	Wetland Area	Species Richness	Shannon- Wiener Diversity Index
SLNC	0.21 km ²	51	1.348
FM	0.04 km ²	30	0.93

Table 3-2. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and sample sizes for all tissues collected from red-bellied turtle (*Pr*) and red-eared slider turtles (*Ts*) between 2008 and 2010 at the Silver Lake Nature Center (SLNC) and at Fort Mifflin (FM). P-values below the 0.05 significance level are highlighted in bold.

Wetland Year	Tissue Type	n		Mean $\delta^{13}\text{C}$ (‰)		Mean $\delta^{15}\text{N}$ (‰)		C p-value	N p-value
		<i>Pr</i>	<i>Ts</i>	<i>Pr</i>	<i>Ts</i>	<i>Pr</i>	<i>Ts</i>		
SLNC 2008	Plasma	12	5	-18.19	-25.92	6.91	9.49	0.002	0.03
	RBC	10	6	-19.18	-26.63	5.56	8.33	0.0002	0.004
	Tail	14	7	-18.26	-24.88	6.57	9.80	0.00007	0.00007
FM 2008	Plasma	7	6	-27.28	-26.20	11.50	12.03	0.11	0.65
	RBC	9	5	-26.66	-25.80	10.31	9.53	0.18	0.23
	Tail	9	6	-26.44	-24.88	10.14	10.81	0.018	0.43
	Filings	7	6	-26.67	-25.35	11.27	10.37	0.004	0.26
SLNC 2009	Plasma	15	4	-19.52	-24.10	7.34	11.60	0.029	0.001
	RBC	12	6	-20.33	-24.30	5.97	9.98	0.001	0.0009
FM 2009	Plasma	16	15	-26.45	-26.90	9.74	10.55	0.42	0.22
	RBC	10	14	-27.14	-26.42	9.74	9.26	0.21	0.35
	Tail	10	12	-25.65	-26.91	9.63	11.12	0.026	0.001
SLNC 2010	Plasma	10	10	-18.46	-23.80	8.25	11.14	0.0002	0.0003
FM 2010	Plasma	10	9	-21.43	-24.87	10.85	11.62	0.19	0.5

Table 3-3. Carbon and Nitrogen stable isotope values for vegetation at Fort Mifflin (FM) and Silver Lake Nature Center (SLNC) during 2010. The values presented are the mean value for all tissue sampled from these plant species. Plants species that were sampled at both wetlands are in bold.

Wetland Complex	Species	Common Name	Mean $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)
FM	<i>Peltandra virginica</i>	Arrow Arum	-28.50	5.15
	<i>Lemna minor</i>	Duckweed	-27.85	10.09
	<i>Myriophyllum spp.</i>	Water milfoil	-16.50	2.24
	<i>Nuphar advena</i>	Spatterdock	-26.86	1.03
	<i>Wolffia spp</i>	Watermeal	-23.64	7.27
SLNC	<i>Amorpha fruticosa</i>	False Indigo	-27.13	0.20
		Swamp		
	<i>Hibiscus moscheutos</i>	Rosemallow	-27.09	8.26
	<i>Lemna minor</i>	Duckweed	-26.49	10.08
	<i>Myriophyllum spp.</i>	Water milfoil	-24.73	9.20
	<i>Nuphar advena</i>	Spatterdock	-26.25	6.10
	<i>Parthenocissus quinquefolia</i>	Virginia Creeper	-28.24	5.67
	<i>Solanum dulcamara</i>	Bittersweet Nightshade	-28.24	10.53
	<i>Viburnum dentatum.</i>	Arrowwood	-26.76	5.39
	<i>Vitis vulpina</i>	Frostgrape	-26.47	7.45
<i>Lyngbia spp.</i>	Filamentous Algae	-19.92	11.02	

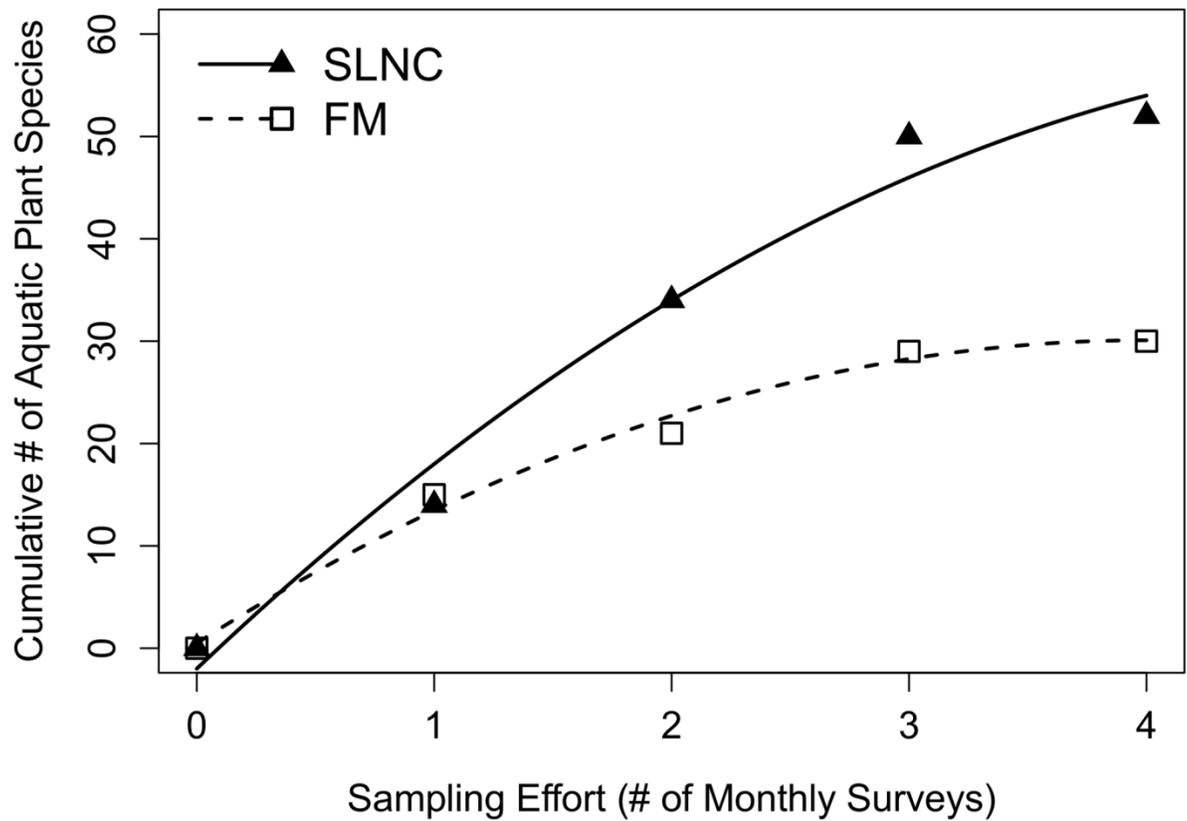


Figure 3-1. Species accumulation curves of aquatic vegetation for the two study sites in 2010. After 4 months of vegetative surveys the number of new species being found at Fort Mifflin (FM) had leveled off while at Silver Lake Nature Center (SLNC) the number of new species had not leveled off. Additional sampling at FM would likely not have found many new species while at SLNC additional sampling would likely result in higher species richness.

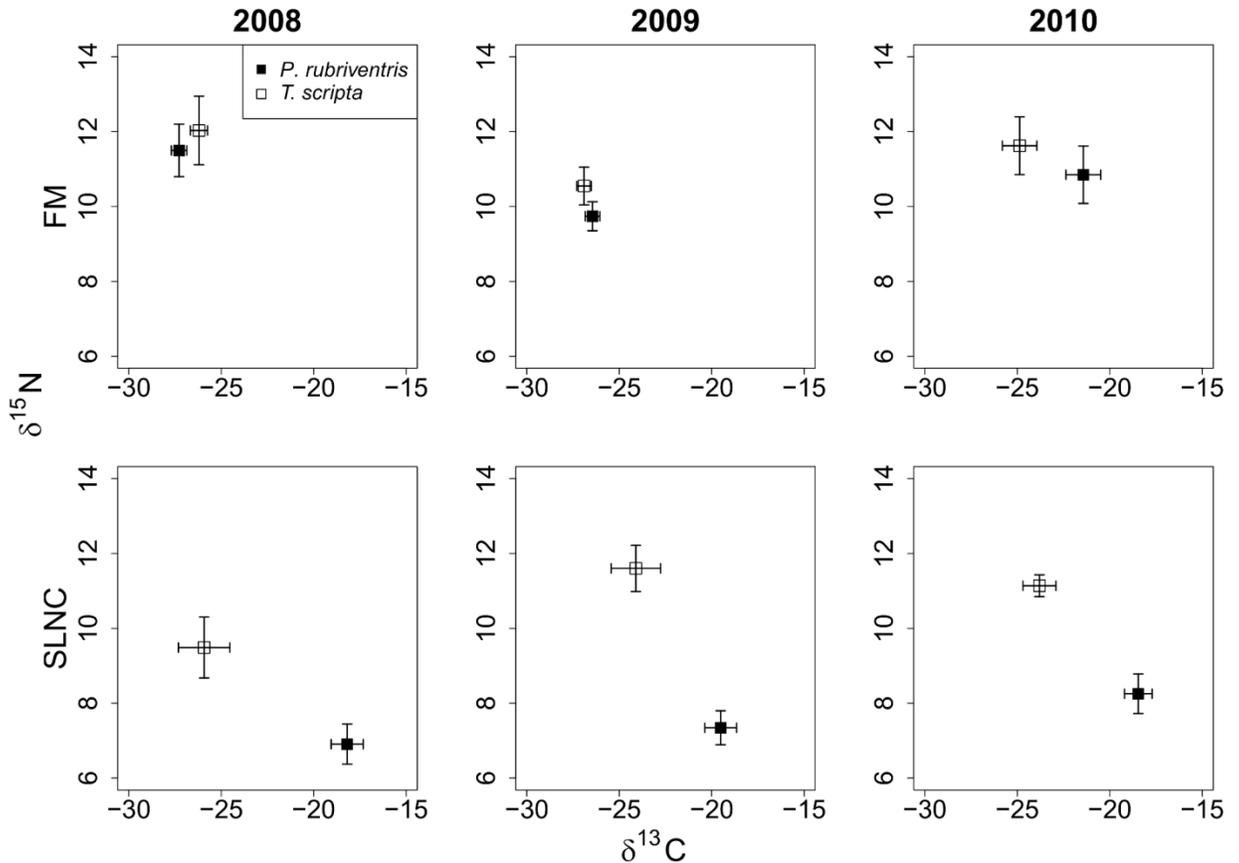


Figure 3-2. $\delta^{13}\text{C}$ (x-axis) and $\delta^{15}\text{N}$ (y-axis) results for blood plasma sampled from red-bellied turtles (closed squares) and red-eared slider turtles (open squares) at the Silver Lake Nature Center (SLNC, bottom row) and Fort Mifflin (FM, top row) for the years 2008, 2009 and 2010. Error bars represent the standard error of the mean. At SLNC there were significant differences for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across all three years. At FM no significant differences were found in $\delta^{15}\text{N}$ values and in 2008 and 2009 no significant differences in $\delta^{13}\text{C}$ values were found.

Supporting Information Legends:

Table S1. Plant species documented during the 2010 resource availability surveys. Plant species found only at FM and SLNC are on the left and right, respectively, while species found at both wetlands are in the center. We documented 31 species at FM and 51 species at SLNC.

FM		FM/SLNC		SLNC	
Species	Common Name	Species	Common Name	Species	Common Name
<i>Amelanchier stolonifera</i>	Running serviceberry	<i>Amorpha fruticosa</i>	False indigo	<i>Acer negundo</i>	Black Maple
<i>Cicuta maculata</i>	Spotted water hemlock	<i>Boehmeria cylindrica</i>	Smallspike false nettle	<i>Acer rubrum</i>	Red maple
<i>Cornus spp.</i>	Dogwood	<i>Carex spp.</i>	Sedge	<i>Acer saccharinum</i>	Sugar maple
<i>Cyperus sculentus</i>	Yellow nutsedge	<i>Cephalanthus occidentalis</i>	Buttonbush	<i>Alnus serrulata</i>	Hazel alder
<i>Hibiscus moscheutos</i>	Swamp rosemallow	<i>Helianthus spp.</i>	Sunflower	<i>Asclepias spp.</i>	Milkweed
<i>Lilium spp.</i>	Lily	<i>Lemna minor</i>	Duckweed	<i>Betula nigra</i>	River birch
<i>Olmus procera</i>	English elm	<i>Lythrum salicaria</i>	Purple loosestrife	<i>Bidens spp.</i>	Beggar-ticks
<i>Rubus spp.</i>	Bramble	<i>Myriophyllum spp.</i>	Water milfoil	<i>Callitriche palustris</i>	Water-starwort
<i>Solanum dulcamara</i>	Bittersweet nightshade	<i>Nuphar advena</i>	Spatterdock	<i>Celastris orbiculatus</i>	Oriental bittersweet
<i>Typha spp.</i>	Cattail	<i>Nymphaea odorata</i>	Fragrant water-lily	<i>Cornus amomum</i>	Silky dogwood
		<i>Onoclea sensibilis</i>	Sensitive fern	<i>Cornus florida</i>	Flowering dogwood
		<i>Parthenocissus quinquefolia</i>	Virginia Creeper	<i>Cuscuta spp.</i>	Dodder
		<i>Peltandra virginica</i>	Arrow arum	<i>Elymus spp.</i>	Wild rye
		<i>Persicaria sagittata</i>	Arrowleaf tearthumb	<i>Euonymus spp.</i>	Spindle tree
		<i>Phragmites australis</i>	Common reed	<i>Gleditsia triacanthos</i>	Honey locust
		<i>Polygonum hydropiper</i>	Marshpepper knotweed	<i>Lonicera japonica</i>	Japanese honeysuckle
		<i>Rhamnus spp.</i>	Buckthorn	<i>Lyngbia spp.</i>	Filamentous algae
		<i>Salix nigra</i>	Black willow	<i>Magnolia tripetala</i>	Umbrella tree
		<i>Viburnum dentatum</i>	Arrowwood	<i>Morus rubra</i>	Red mulberry
		<i>Vitis vulpina</i>	Frostgrape	<i>Pinus strobus</i>	Eastern white pine
		<i>Wolffia spp.</i>	Watermeal	<i>Platanus occidentalis</i>	American sycamore
				<i>Potamogeton confervoides</i>	Tuckerman's pondweed
				<i>Quercus palustris</i>	Pin oak
				<i>Rhus typhina</i>	Staghorn sumac
				<i>Rosa multiflora</i>	Multiflora rose
				<i>Spiraea spp.</i>	Steeplebush
				<i>Syringa spp.</i>	Lilac
				<i>Tilia americana</i>	American basswood
				<i>Ulmus americana</i>	American elm
				<i>Valeriana spp.</i>	Valerian

CHAPTER 4: Invasive Red-eared slider turtles negatively impact the growth of native turtles: Implications for global freshwater turtle populations

Abstract

Invasive species are a significant cause of biodiversity declines on a global scale with novel species interactions often causing ecological damage through predation or competition. The red-eared slider turtle (*Trachemys scripta elegans*) has been introduced to wetlands throughout the world and negatively impacts native species, particularly other turtle species. In controlled feeding experiments in mesocosms red-eared slider turtles negatively impacted the growth of red-bellied turtles (*Pseudemys rubriventris*), a North American species, through exploitative competition for limited food. When food resources were abundant red-bellied turtles grew significantly faster and ate more food than red-eared slider turtles in mixed species groups. When food resources were limited red-eared slider turtles ingested more food, gained mass faster, and maintained body condition while red-bellied turtles lost body condition. My results suggest that the mechanism by which red-eared slider turtles detrimentally impact ecologically similar species is through competition for limited food resources. I hypothesize that growth of red-eared slider turtle populations will lead to population declines of native turtle species throughout their introduced ranges because they can more efficiently use limited food resources for their growth and development than native species.

Introduction

Invasive species can negatively impact the fitness of native species through predation or competition (Alison et al. 1995, Schoener and Spiller 1996). Predation can have immediate negative effects and can lead to the collapse of entire faunas (Schoener and Spiller 1996, Rodda et al. 1997) while the effects of competition are often delayed (Petren and Case 1996) and exacerbated or perturbed by concurrent events such as habitat alteration (Davis 2003). To determine the long term, delayed effects of competition between species it is necessary to determine whether an introduced species shares resources with native species (Polis and McCormick 1987) and if there are reductions in the growth rates, reproductive rates or survivorship of at least one of the species (Polis and McCormick 1987, Amarasekare 2002). Natural experiments, which determine resource use of wild organisms, coupled with controlled experiments that determine the mechanisms of competition, should be utilized to determine the potential for competition between wild animals and the mechanisms by which species compete.

Within an established ecological community, species obtain a realized niche by partitioning available resources and limiting the extent of resource overlap between species (Austin et al. 1990, Shea and Chesson 2002). Resource overlap that occurs between native species and introduced species may result in an alteration of a native species realized niche (Austin et al. 1990, Shea and Chesson 2002), which may lead to reduced fitness through growth, survival and/or reproductive rates of competing species (Polis and McCormick 1987). The effects of resource limitations on fitness can be demonstrated when fitness metrics are different between high and low resource

environments. Furthermore, the effects of competition can be demonstrated when fitness metrics are suppressed by the presence of a competitor (Polis & McCormick 1987).

An organism's fitness can be inferred in several ways. Classic metrics of life history traits such as growth, fecundity and survivorship are all used to estimate an organism's fitness (Schmidt and Levin 1985, Stearns et al. 2000). In addition, the Body Condition Index (BCI) has been used to estimate short-term shifts in an organism's overall health and to infer instantaneous fitness levels throughout different stages of an organism's life (Wallis et al. 1999, Shine et al. 2001, Litzgus et al. 2008).

Here, I report the results of an experiment in which an invasive species, the red-eared slider turtle (*Trachemys scripta elegans*), was competitively superior to a native species, the red-bellied turtle (*Pseudemys rubriventris*), under low resource conditions. The experiments detailed below are useful in understanding the mechanisms by which red-eared slider turtles may be causing reductions in the long term growth, reproduction or survivorship of red-bellied turtles.

Methods

Study species

Red-eared slider turtles (*Trachemys scripta elegans*) are native to the Mississippi River Valley of the United States with a broad distribution between Texas in the south and Illinois in the north (Ernst et al. 1994). Red-eared slider turtles are the most widely introduced turtle species with a current global distribution on all continents except for

Antarctica (Lever 2003). They are often introduced through the pet trade, as escaped food items or for religious purposes (Ng et al. 2005, Ramsay 2007). In Europe red-eared slider turtles have been shown to negatively impact native species including the European Pond turtles (*Emys orbicularis*) and the Spanish terrapin (*Mauremys leprosa*) (Polo-Cavia et al. , Cadi and Joly 2003, 2004, Polo-Cavia et al. 2009a). This species may negatively impact many other turtle species within their introduced range. In the coastal plain of the mid-Atlantic region of the United States the red-bellied turtle (*Pseudemys rubriventris*) is an ecologically similar turtle that may be negatively impacted by red-eared slider turtles (Stone 2010, Pearson et al. 2013).

Red-bellied turtles are native to the Atlantic coastal plain of the United States between Massachusetts in the north and North Carolina in the south (Ernst et al. 1994). Across the northern portion of this species range, population have declined and the current distribution is from approximately New York City, NY south to North Carolina (Waters 1962, Ernst et al. 1994). In Pennsylvania this species has declined across its range with recent surveys documenting red-bellied turtles only in 50% of wetlands with historical records (Stone 2010). Red-bellied turtles and red-eared slider turtles overlap for dietary resources in some wetlands but partition dietary resources in other wetlands (Pearson et al. 2013). If shared resources become limiting, competition for resources will occur and the species that is a better competitor for those limited resources will negatively impact the growth, reproduction or survivorship of the inferior competitor.

Experimental design

I conducted experiments with juvenile one year old turtles purchased from the Turtle Shack, a commercial breeder, Port Richey, FL. Each of three experimental replicates consisted of six treatments that were designed to test for intra- and inter-specific competition by altering the species composition and amount of resources available per turtle. Resource availability was experimentally manipulated by maintaining equal amounts of resources (i.e. aquatic environment (~710 L), basking space (0.024 m²) and food (100 pellets/feeding event) while altering the number of turtles in each resource availability regime. The experiment was performed on the northwestern edge of an open lawn, separated from an adjacent livestock field by a single row of mature black cherry trees and an electric fence. The position alongside this windbreak enabled the experimental tanks to receive morning sun and to be shaded in the afternoon. All experimental procedures were approved by Drexel University I.A.C.U.C. protocol #19735.

Each experiment consisted of low resource availability groups which had twelve turtles and high resource availability groups which had six turtles. Resource availability manipulations are discussed below. Within resource availability groupings there were experimental treatments which consisted of two conspecific groups (i.e. a red-bellied turtle only group and a red-eared slider turtle only group) and a mixed species group comprised of a 1:1 ratio (Figure 1).

Husbandry

Experimental enclosures were 1.83 m diameter polyethelene tanks and contained a single basking site that measured 13.5 cm x 18 cm. This size basking platform was large enough to fit 100% of the turtles within the high resource availability treatments but only 50% of turtles in low resource availability treatments. Water level was maintained at approximately 27 cm but varied slightly between tanks such that the surface of the basking platform remained above water. Enclosures were covered with 80% shade cloth during all times except for 4 hours on Monday, Tuesday, Thursday and Friday during feeding and basking events and for up to 8 hours on Wednesdays while enclosures were being cleaned and turtles measured. Shade cloth covers were used to keep potential food items (e.g. insects, fruit) and predators (e.g. birds, raccoons) from entering the enclosures. In addition shade cloth covers limited aerial basking opportunities and reduced water temperatures. Enclosures were skimmed daily to keep the water free of debris, thus ensuring that no additional food items were available. Enclosures were emptied and sanitized weekly with bleach and scrubbed clean to eliminate algal growth, a potential food. Weekly water changes also limited waste and kept water temperatures lower encouraging the use of the basking sites. Water temperatures fluctuated with ambient temperature and if it reached 34°C for a 24 hour period it was replaced with cool water. While experimental enclosures were being cleaned, each turtle was dried with a towel, measured, and weighed. Measurements included carapace length, carapace width, carapace height, plastron length and mass. All length measurements were to the nearest 0.1 mm and were made using a Control Company, Model # 3418 digital caliper. Mass

was measured to the nearest 0.01 gram with an OHAUS Scout Pro digital balance. Measurements were all taken by the same researcher (SHP) throughout the experiment.

Acclimatization Period

Turtles were randomly selected and marked with a unique notch code filed into the marginal scutes. Turtles were then randomly assigned to an experimental replicate and treatment. Turtles were placed in their experimental enclosures and acclimatized to the experimental conditions for a 21 day period. During the first 14 days of acclimatization the amount of food consumed by turtles fed *ad lib* was determined by calculating the number of individual pellets consumed during a 45 minute feeding period by each treatment. Results from the *ad lib*. feeding periods were used to determine how much food an experimental treatment was expected to consume if food resources were not limiting. After 14 days of *ad lib*. feeding, experimental treatments were switched to the experimental feeding regime which consisted of *ad lib*. feeding for high resource groups and a 50% reduction in *ad lib*. feeding amount for low resource groups. A 50% reduction for low resource treatments was achieved by feeding all treatments enough food for the average group of six turtles to feed at *ad lib* levels. During the acclimatization period, turtles were exposed to the full suite of experimental procedures.

Feeding Regime

On Monday, Tuesday, Thursday and Friday all treatments within a replicate were fed simultaneously with Zoo Med turtle food - growth formula. All feeding occurred between 8 am and 12:00 pm. One hundred pellets were placed in an indentation

approximately 3.5 cm x 10.5 cm, centered on the feeding/basking platform, and turtles were left to eat for 45 minutes undisturbed.

Individual turtle ingestion

Prior to food being placed on the platform a camera from an eight-camera digital security system was suspended directly above the feeding platform with cables run to a remote DVR. Each camera's position was checked using an LCD screen attached to the DVR to ensure that the view being recorded was of the feeding platform and the surrounding water. The DVR recorded and named all files. Upon review individual turtle ingestion was determined by tallying every time a turtle climbed onto the platform and successfully re-entered the water with a pellet in beak. If a turtle was known to eat a pellet obtained by other means it was also tallied with an additional pellet.

Calculations and Data Analysis

Growth Rates and Body Condition Indices

I used weekly measurements to calculate growth rates and body condition indices for individual turtles. I calculated individual turtle growth rates using linear regression on the plastron length and mass over the experimental duration (11 weeks). Mean growth rates for experimental treatments were used for further analyses. Body condition indices were calculated using the method described in Wallis et al. (1999), which divides body mass (g) by the turtle's volume. Turtle volume can be calculated either as the carapace length cubed or as the product of carapace length, carapace width and carapace height

(Wallis et al. 1999). Similarly to Wallace et al (1999), my results do not differ between method and I report the results using carapace length cubed (Wallis et al. 1999).

Data Analysis

Growth rate

I first examined the individual growth rates of each turtle to determine if the growth rates of turtles were linear over the eleven week period of my experiment. I did not log transform data due to the linear relationship found for all of the growth metrics (i.e. length, mass and body condition) and time. I next determined significant differences between growth rates of experimental groups using Linear Mixed Effect (LMER) models. The LMER contained Plastron Length (PL), Mass or Body Condition Index (BCI) as the response variables and the interaction between treatment and weekly measurements as the fixed effects. The random effects of the LMER were the experimental blocks (replicates) and individual turtle IDs with variation in the intercept of the slope between weekly measurement events. I determined significant differences between groups by fitting reduced models that omitted factors and testing whether those omissions significantly degraded the predictive power of the model as measured by AIC and p-values (Quinn and Keough 2008). All statistical analyses were performed in Program R (R Development Core Team 2011); Linear mixed effect models were run with LMER in the LME4 package (Bates and Maechler 2009).

Ingestion

Using two-way ANOVA I determined if there were significant differences between ingestion rates by replicates and or species. In cases in which significant differences existed between replicate I determined which replicates were significantly different from one another by fitting a reduced model which omitted a replicate and tested whether that reduced model significantly increased the predictive power of the model. For results without significant differences between replicates I used the combined means to determine if there were differences between species. For results with significant differences between replicates I tested non-significantly different replicates together using two-way ANOVA and significantly different replicates by themselves using two-tailed student t-tests to determine if the experimental results were the same, even though the mean number of pellets ingested differed from other replicates.

Results

Growth Rates

Growth in plastron length ranged from a mean of 0.2 mm/week in red-bellied turtles housed alone in the low resource availability treatment to 0.58 mm/week in red-bellied turtles and red-eared slider turtles housed in the mixed species high resource and single species high resource treatment, respectively (Table 1). Growth in mass ranged from a mean of 0.79 g/week in red-bellied turtles housed in the low resource treatments to 1.79 g/week in red-bellied turtles housed in the mixed species high resource treatment. Changes in body condition index (BCI) ranged from $-0.0005\text{g}/\text{cm}^3$ for red-bellied turtles

housed with red-eared slider turtles in the low resource treatment to 0.0007 g/cm^3 for red-eared slider turtles housed with red-bellied turtles in the low resource treatment.

Comparisons between resource availability groups

Red-bellied turtles grew significantly faster as measured by plastron length, mass and body condition index in high resource treatments than in low resource treatments in mixed species groups (Table 2, Figure 1). There were no statistically significant differences in growth rates of red-eared slider turtles as measured by plastron length, mass and body condition index in low resource or high resource treatments in mixed species groups (Table 2, Figure 1)

Both red-bellied turtles and red-eared slider turtles grew significantly faster as measured by both plastron length and body mass in high resource treatments than in low resource treatments, when housed alone (Table 2, Figure 1). There were no significant differences in body condition index between red-bellied turtles or red-eared slider turtles housed with conspecifics in low resource vs. high resource treatments (Table 2, Figure 1).

Comparisons within resource availability groups

Under low resource conditions red-bellied turtles body condition changed significantly faster when housed with conspecifics than when housed with red-eared slider turtles (Table 1 & 3, Figure 1). Under the same low resource conditions, red-eared slider turtles grew faster, as measured by both mass and body condition, when housed in mixed species groups than when housed with conspecifics (Table 1-3, Figure 1). Red-

red-eared slider turtles grew significantly faster, as measured by all three measures, than red-bellied turtles when in mixed species groups under low resource conditions (Table 1 & 3, Figure 1).

Under high resource conditions there were no statistically significant differences in growth rates in red-bellied turtles or red-eared slider turtles when housed with conspecifics. Red-bellied turtles grew significantly faster, as measured by plastron length and mass, than red-eared slider turtles when housed in mixed species groups under high resource conditions (Table 1 & 3, Figure 1).

Ingestion Rates

Red-eared slider turtles consumed more food pellets than red-bellied turtles when they were housed in mixed species groups in low resource conditions ($F=24.12$, $p<0.0001$, $df=1$). However, red-bellied turtles ate more pellets than red-eared slider turtles when they were housed in mixed species groups in high resource conditions ($F=8.14$, $p=0.005$, $df=1$, Table 4). There were no significant differences between the number of pellets consumed by red-bellied turtles or red-eared slider turtles housed alone in either high resource groups ($F = 1.9$, $p = > 0.1$, $df = 1$) or low resource groups ($F = 0.194$, $p = 0.66$, $df = 1$). (Table 2, Figure 2).

Discussion

In controlled feeding experiments in mesocosms, red-eared slider turtles negatively impacted the growth of red-bellied turtles. When food resources were limited

red-eared slider turtles ingested more food, gained mass faster and maintained body condition, while red-bellied turtles experienced decreases in body condition. Therefore, when food resources were limited red-eared slider turtles outcompeted red-bellied turtles for food. When housed in single species mesocosms, red-eared slider turtles grew slower than they did in mixed species groups, suggesting that intraspecific competition reduced their ability to obtain food. In high resource conditions red-bellied turtles grew faster than red-eared slider turtles when housed together. This suggests that under the experimental conditions red-bellied turtles have an inherent ability to grow faster than red-eared slider turtles when food was not limited and competition was reduced.

The growth rates that I measured were below the maximum potential growth rates for both species. Juvenile red-bellied turtles can grow up to 0.78 mm/wk plastron length (Graham 1971, Haskell et al. 1996) and juvenile red-eared slider turtles can grow up to 1.2 mm/wk plastron length (Avery et al. 1993, Ernst et al. 1994, McRobert and Hopkins 1998).

Interspecific competition can be inferred when fitness metrics are reduced across a resource availability gradient in the presence of a second species but not in the presence of conspecifics (Polis and McCormick 1987). My experimental results suggest that interspecific competition is important because red-bellied turtles were inherently a faster growing turtle than red-eared slider turtles yet were negatively impacted in mixed species groups when resources were limited. These experimental results coupled with previous research on red-eared slider turtles and native species in Europe (Cadi and Joly 2003,

2004, Polo-Cavia et al. 2009a) have implications for the community ecology of freshwater turtles throughout the world.

Mechanism for impacting native species

In aquatic systems, red-eared slider turtles are a successful invader, naturalized on all continents except for Antarctica, are thought to be negatively impacting native species throughout their introduced range (Lever 2003) and have been shown to negatively impact other turtle species in highly controlled experiments such as those performed by Polo-Cavia *et al.* (2009, 2010) with the Spanish Terrapin, and in more natural experiments such as those performed by Cadi and Joly (2003) and Polo-Cavia *et al.* (2010). In the experiment detailed here and in those of Polo-Cavia *et al.* (2010) red-eared slider turtles ingested more food when competing for food with other species than with con-specifics. Furthermore, in my experiment and those of Cadi & Joly (2003) red-eared slider turtles in mixed species groups continued to gain mass and maintain body condition but the other species with which they were being housed lost mass and body condition. In Cadi and Joly's (2003) extended duration experiments these interactions resulted in decreased survivorship of the other species. Polo-Cavia et al. (2009, 2010) report that individual Spanish terrapins reduce time spent basking in the presence of individual red-eared slider turtles and that individual red-eared slider turtles ingest more food when a Spanish terrapin was present as compared to when another red-eared slider turtle was present. The results from Polo-Cavia *et al.* (2010) trials with individual turtle pairs are similar to those found within my experimental groups. In both Cadi and Joly (2003) and Polo-Cavia (2009), red-eared slider turtles were stronger competitors for

limited basking sites than either European pond turtles or Spanish terrapins (Cadi and Joly 2003, Polo-Cavia et al. 2009a).

The findings from Cadi and Joly (2003, 2004), Polo-Cavia *et al.* (2009, 2010) and this study indicate that red-eared sliders primarily impact other ecologically similar turtle species within their introduced range by exploitative competition for dietary resources in environments with limited resources. Field studies of red-eared slider turtle distributions and diets indicate that they can share spatial and dietary resources with other ecologically similar species (Thomson et al. 2010, Pearson et al. 2013). Red-eared slider turtles may alter the habitat use and distributions of other species (Polo-Cavia et al. 2009b) through exploitative or interference competition for basking sites (Polo-Cavia et al. 2009b).

Experimental and ecological data between red-eared slider turtles and other native turtle species are sufficient to propose a mechanism for how red-eared slider turtles may negatively impact native species throughout their introduced range. Under experimentally controlled conditions with limited resource availability, red-eared slider turtles are stronger competitors than European pond turtles, red-bellied turtles and Spanish terrapins, all ecologically similar species. If the results of these varied experiments hold true in natural environments then I expect that red-eared slider turtles would negatively impact the long term growth of European pond turtles, red-bellied turtles, Spanish terrapins and other ecologically similar species throughout their introduced range. Reduced growth rates in turtles can result in reduced lifelong fecundity as a result of delayed time to maturity and decreased clutch size (Congdon and Gibbons

1985, Avery et al. 1993, Litzgus et al. 2008). In habitats where populations of red-eared slider turtles have become established and other ecologically similar species are present then I suspect that in periods of resource limitations red-eared slider turtles are inherently better suited to obtain resources due to a more aggressive nature of resource consumption. Specifically, if wild red-bellied turtles grow at a slower rate when living sympatrically with red-eared slider turtles than they would if red-eared slider turtles were not present, then the long-term result of red-eared slider introductions will be reduced lifelong fecundity for red-bellied turtles. Decreased growth rates could lead to a decline in recruitment, population size and long term persistence of red-bellied turtles (Congdon et al. 1993).

Human land use practices and population density is highly correlated with increases in species introductions (Spear et al. 2013) and habitat fragmentation (Andr n 1994). Furthermore, as human density and habitat fragmentation increases resource overlap between species tends to also increase as habitat availability and resource availability decrease (Fahrig 2003, Swihart et al. 2003b). Introduced red-eared slider turtle populations tend to be associated with human population density and anthropogenically impacted wetlands (Stone 2010, Thomson et al. 2010). In sympatric populations of red-bellied turtles and red-eared slider turtles, smaller more fragmented wetlands led to increased dietary resource overlap between these two species (Pearson et al. 2013). If wild red-eared slider turtles are better competitors than ecologically similar species, such as the red-bellied turtle, then in highly impacted or fragmented wetland landscapes in which resource limitations occur red-eared slider turtles would more

efficiently obtain limited resources and their populations could increase more rapidly than native species. My experimental findings if applied at broader ecological scales such as the mid-Atlantic Coastal Plain of the United States, or any region with dense populations of humans, suggests that red-eared slider turtles can negatively impact ecologically similar species and alter the species composition of ecosystems over a regional scale. Further studies of wild populations are needed to determine the broad scale implications of my findings.

Resource availability differences

In my experiments I found that red-eared slider turtle growth rates did not respond to the alteration of dietary resources available. In both high resource groups that contained red-eared slider turtles and in the low resource mixed species groups the mean number of pellets consumed per red-eared slider turtle remained the same suggesting that red-eared slider turtles are more aggressive consumers than red-bellied turtles when resources are limited. Under abundant resource conditions and in low resource mixed species groups red-eared slider turtles consumed the same number of pellets. In low resource single species groups the number of pellets per red-eared slider was reduced due to intra-specific competition. Previous studies of red-eared slider turtles have determined that this species experiences differential growth rate under different resource regimes and environmental variables (Webb 1961, Gibbons 1970, Gibbons et al. 1981, Dunham and Gibbons 1990, Avery et al. 1993). For example Gibbons et al. (1981) showed that red-eared slider turtles in Par Pond, a high resource environment, grew more rapidly than those in Ellenton Bay which was a low resource environment. Studies performed with

wild turtle populations varied in resource availability and in resource quality with environmental conditions such as the thermal effluent of nuclear reactors (Gibbons 1970). My experimental results may differ from those with wild populations because I was able to control environmental conditions and manipulate resource availability. The non-differentiated growth rates between red-eared slider turtles in high resource and low resource mixed species groups suggest that red-eared slider turtles outcompete red-bellied turtles in limited resource environments while the different growth rates between red-eared slider turtles in low resource and high resource single species groups suggests that intra-specific competition retards the growth of each other in the presence of conspecifics.

Conservation Implications

The continued introduction of invasive species across the globe is of concern to researchers, conservationists and managers on all continents (Pimentel et al. 2005, Lockwood et al. 2007). Red-eared slider turtles are one example of globally distributed species which may impact native species within their introduced range (Lever 2003, Cadi and Joly 2004, Ng et al. 2005, Ramsay 2007, Outerbridge 2008). Specifically, red-eared slider turtles may be negatively impacting the growth of individual turtles, the recovery of turtle populations as well as other unknown impacts as they disturb ecologically established communities. More generally, indirect interactions between invasive species and native species, such as through competition for resources, can lead to reduced fitness rates for native species potentially leading to long term, persistent declines in populations (Byers 2000).

The combination of my experimental results with those found by other researchers strongly indicate that red-eared slider turtles are capable of causing ecological damage to native species. Management efforts should be made to reduce the number of introductions of red-eared slider turtles and other invasive species that occur on a global scale. Reductions in the number of non-native pets being sold should be mandated while the intentional introduction of non-native species should also be prohibited.

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Table 4-1. Growth rates of red-bellied turtles (*Pr*) and red-eared slider turtles (*Ts*) grown in experimental mesocosms under low resource mixed species (LRMS), low resource single species (LRSS) conditions, high resource mixed species (HRMS) and high resource single species (HRSS) conditions.

	LRMS		LRSS		HRMS		HRSS	
	<i>Pr</i>	<i>Ts</i>	<i>Pr</i>	<i>Ts</i>	<i>Pr</i>	<i>Ts</i>	<i>Pr</i>	<i>Ts</i>
Plastron Length (mm/wk)	0.28	0.41	0.20	0.40	0.58	0.50	0.38	0.58
Mass (g/wk)	0.79	1.09	0.79	0.99	1.79	1.20	1.29	1.45
Body Condition Index	-5.3×10^{-7}	7.5×10^{-7}	1.5×10^{-7}	4.6×10^{-7}	6.5×10^{-7}	6.7×10^{-7}	2.0×10^{-7}	7.3×10^{-7}

Table 4-2. P-values obtained through comparisons between Linear Mixed Effect Models and null models of Plastron Length (PL), Mass and Body Condition Index (BCI) for low resource groups (LR) and high resource groups (HR) in mixed species red-bellied turtle (MS-*Pr*), mixed species red-eared slider turtle (MS-*Ts*), single species red-bellied turtle (*Pr*) and single species red-eared slider turtle (*Ts*) treatments. Statistically significant results are highlighted in bold.

	LR-MS<i>Pr</i> – HR-MS<i>Pr</i>	LR-MSTs – HR-MSTs	LR-<i>Pr</i> – HR-<i>Pr</i>	LR-<i>Ts</i> – HR-<i>Ts</i>
PL	0.007	0.297	0.013	0.005
Mass	0.002	0.593	0.049	0.002
BCI	<0.001	0.767	0.808	0.163

Table 4-3. P-values obtained through comparisons between Linear Mixed Effect Models and null models of Plastron Length (PL), Mass and Body Condition Index (BCI) for growth rates between red-bellied turtles (*Pr*) housed in low resource mixed species groups and single species groups, red-eared slider turtles (*Ts*) housed in low resource mixed species groups and single species groups, red-bellied turtles and red-eared slider turtles raised together in low resource conditions, red-bellied turtles housed in high resource mixed species groups and single species groups, red-eared slider turtles housed in high resource mixed species groups and single species groups and red-bellied turtles and red-eared slider turtles raised together in high resource conditions.

	Low Resource			High Resource		
	Within Species		Between Species	Within Species		Between Species
	<i>Pr</i> Mixed / Single	<i>Ts</i> Mixed / Single	<i>Pr &Ts</i> Mixed	<i>Pr</i> Mixed / Single	<i>Ts</i> Mixed / Single	<i>Pr &Ts</i> Mixed
(PL)	0.17	0.73	0.007	0.14	0.32	0.008
(Mass)	0.97	0.03	<0.001	0.23	0.19	<0.001
(BCI)	<0.001	0.004	<0.001	0.22	0.802	0.76

Table 4-4. Average number of pellets consumed by turtle within experimental groups during feeding periods. Data were collected by reviewing digital video of feeding turtles. Statistically significant differences between species are highlighted in bold.

	Low Resource		High Resource			
	Mixed	Single	Mixed		Single	
			Replicate 1,2	Replicate 3	Replicate 1,2	Replicate 3
<i>P. rubriventris</i>	5.8	5.9	10.7	9.2	8.5	6.8
<i>T. scripta</i>	7.2	6.0	8.7	4.6	7.8	7.5
P-value	<0.001	0.64	0.005	<0.001	0.2	0.1

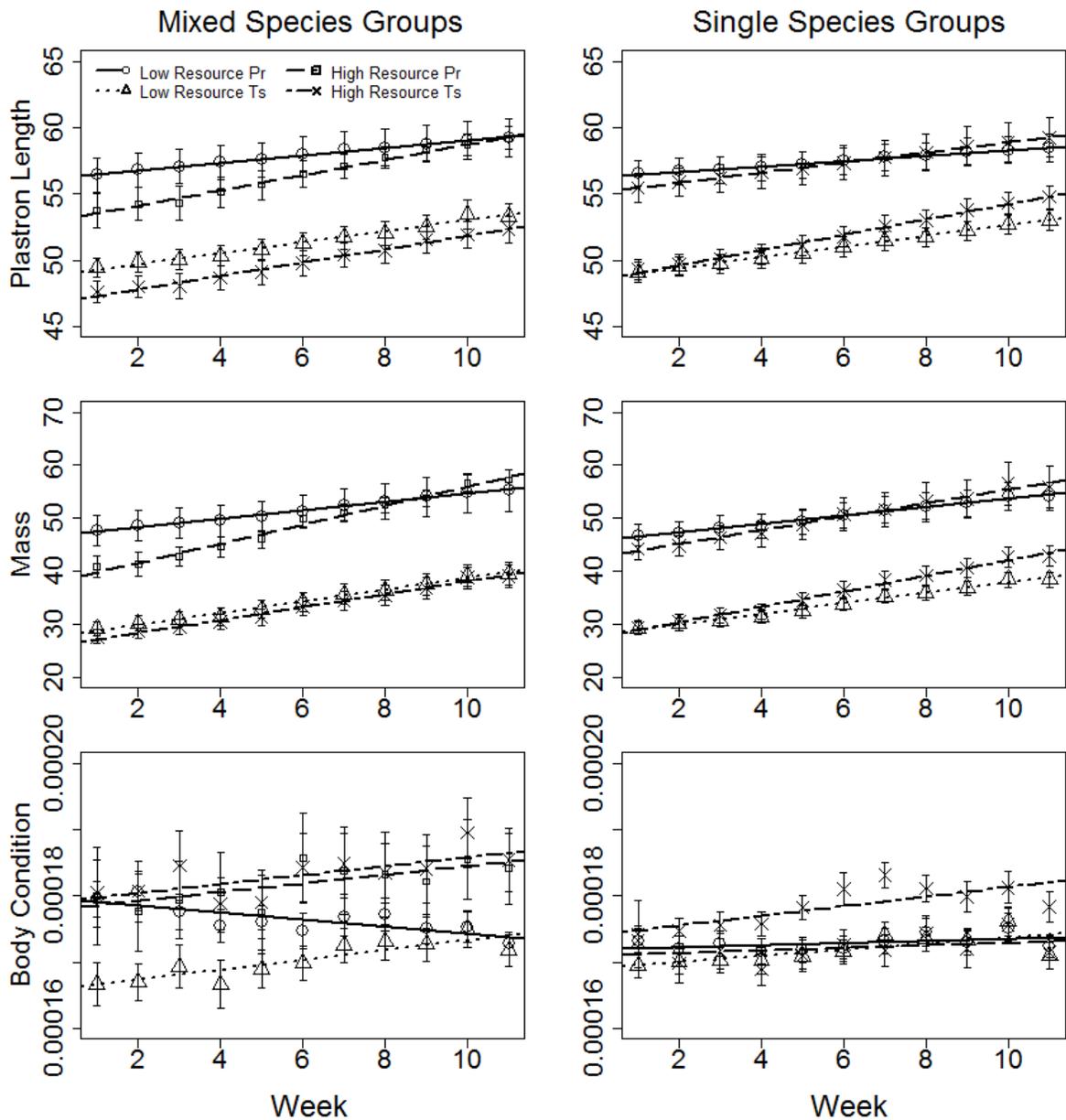


Figure 4-1. Mean weekly measurements of plastron length, mass and body condition for each experimental treatment. Mixed species groups are shown in the left column and single species group in the right. Linear regressions indicate each experimental groups mean growth rate. Low resource red-bellied turtles (Pr) are shown with open circles and high resources red-bellied turtles are indicated by the open squares. Low resource red-eared slider turtles (Ts) are shown with open triangles and high resource red-eared slider turtles are indicated by the x. Error bars indicate the standard error of the mean.

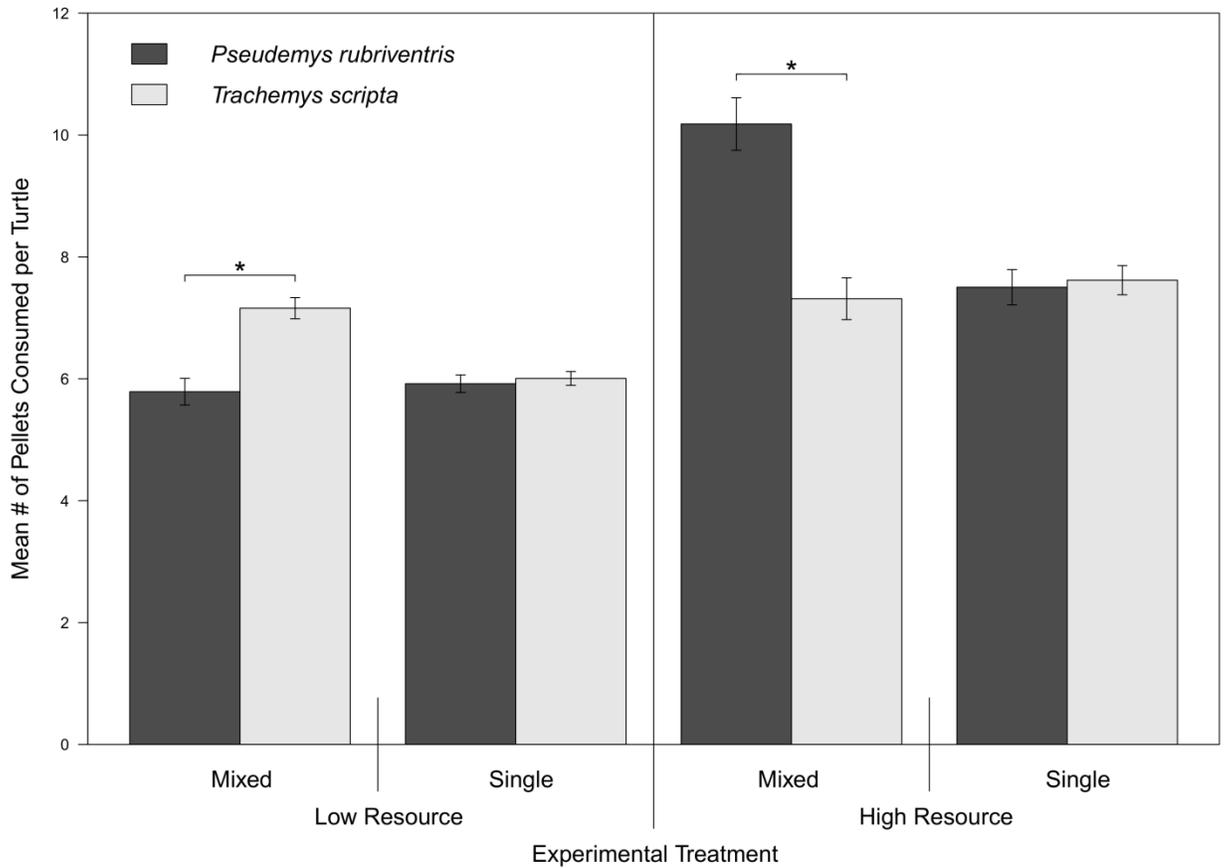


Figure 4-2. Mean number of pellets consumed per turtle during feeding periods. Red-bellied turtles are shown in dark grey and red-eared slider turtles are shown in light grey. Statistical differences existed between species in mixed species groups but not in single species groups.

CHAPTER 5: Dissertation Summary and Conservation Implications

Introduction

Invasive species can impact native species in numerous ways that can be immediate, as is in the case of invasive predators and pathogens, or delayed, as is the case with invasive competitors. The effects of direct interactions between species are easily seen through rapid changes in abundance or behavior. When interactions between native and introduced species are indirect it can be difficult to determine whether or not an introduced species is negatively impacting the fitness of another species because shifts in abundance or behavior occur on slower timescales. If negative impacts on the fitness, abundance or distribution of a species are suspected both field studies and experiments are useful tools to elucidate the types of ecological interactions that occur between species. Through studying wild populations we learn how organism's use the environment and which resources they share in common. Through controlled experiments we can determine mechanisms by which one species can impact another.

This dissertation has detailed a series of studies that sought to determine the extent of resource overlap and the potential for competition between wild populations of introduced red-eared slider turtles and the native red-bellied turtle in two wetland complexes. In addition the dissertation details an experiment which manipulated environmental variables to determine if red-eared slider. The major findings from each chapter are detailed below.

Spatial overlap by wild turtles

Red-eared slider turtles (*Trachemys scripta elegans*) and red-bellied turtles (*Pseudemys rubriventris*) live sympatrically in wetlands across the southeastern Pennsylvania region (Stone 2010) and likely throughout the entire red-bellied turtle range. In the two wetland complexes that I studied in detail both red-bellied turtles and red-eared slider turtles used the aquatic area available in a similar manner. Both species utilized the entirety of the wetland and thus may interact more intimately for other resources within these wetland complexes. Individual turtles varied in the extent of the habitat used with individual from both species being documented only in small regions while other individuals were documented throughout the entire wetland complex. Across southeastern Pennsylvania there are many other wetlands in which red-eared slider turtles and red-bellied turtles are living sympatrically (Stone 2010). It is likely that in any wetland in which red-bellied turtles and red-eared slider turtles co-exist that both species use the environment in similar manners. If these species co-exist and share resources then the potential for competition between these species exists as they would be sharing resources in the same place and time.

Dietary overlap by wild turtles

Red-eared slider turtles and red-bellied turtles had overlapping diets in one wetland but partitioned diets in a second wetland. These wetlands differed in the wetland characteristics of size, vegetative species richness and vegetative species diversity with increased overlap for dietary resources occurring in smaller and more vegetative depauperate wetlands while partitioning of resources occurred in the larger and more

species rich wetland. These differences indicate that there are habitat dependent differences in resource overlap between red-eared slider turtles and red-bellied turtles. These differences may have long term implications on the success of red-eared slider turtles or the recovery of red-bellied turtle populations depending on which species obtains necessary resources in times of resource limitations. Wetlands are dynamic habitats with seasonal fluctuations in dietary items available for consumption by turtles and other organisms. In wetlands where extensive overlap for dietary resources occurs it is likely that at some point in time resources will become limiting and that the species which is a better competitor for those limited resources will obtain them and that the weaker competitor will be negatively impacted through reduced growth, survivorship or reproduction. If competition is persistent then the affects may be noticeable within the short term and manifest in terms of reduced health, growth and lower reproduction in the next period. If competition is sporadic then the affects may only be realized on the long term and manifest in terms of reduced growth rates or life time reproduction.

Red-eared slider turtles competitive abilities

Manipulative experiments with red-eared slider turtles and red-bellied turtles determined that red-eared slider turtles are competitively superior to red-bellied turtles in resource limited environments. Red-eared slider turtles were not inherently faster growing turtles than red-bellied turtles as red-bellied turtles grew at a faster rate than red-eared slider turtles when resources were abundant. However, red-eared slider turtles were competitively superior to red-bellied turtles in resource limited environments. Under low resource conditions red-bellied turtles had reduced body condition when

raised with red-eared slider turtles as compared to when raised with conspecifics. If the competitive abilities of red-eared slider turtles in the manipulated resource limited environments is replicated in natural environments then the long term impact of red-eared slider turtle introductions to wetlands with red-bellied turtles could be reduced growth, and survivorship of individual turtles and of whole populations. Extrapolating the results of the manipulative experiments to wild populations should be done with caution but may be instructive in better understanding how introduced red-eared slider turtle populations may impact red-bellied turtles.

Synthesis

In wild populations adult red-eared slider turtles and red-bellied turtles utilized the same habitats in several wetlands yet the extent of dietary overlap depended on the characteristics of those wetlands. In manipulative experiments with juvenile turtles red-bellied turtles grew at a significantly faster rate than red-eared slider turtles when resources were abundant yet when resources were limited red-bellied turtles had reduced growth rates and red-eared slider turtles grew at a significantly faster rate than red-bellied turtles. These results strongly indicate that juvenile red-eared slider turtles are competitively superior to juvenile red-bellied turtles and suggest that in wild populations juvenile red-eared slider turtles should also be competitively superior to juvenile red-bellied turtles.

There remains a disconnect between the results of my field studies of adult turtles and the manipulative studies with juvenile turtles which weakens our ability to

extrapolate the results from the manipulative experiments to wild populations. If adult turtles interact similarly to juveniles then it is likely that adult red-eared slider turtles would be competitively superior to adult red-bellied turtles because red-eared slider turtles are a generalist and aggressive species while red-bellied turtles are less so (Ernst et al. 1994, Polo-Cavia et al. 2009a). To be certain that adult red-bellied turtles and adult red-eared slider turtles would respond to resource limited environments in the same manner as juveniles did additional studies with adult turtles should be conducted. Further research into the interactions of adult turtles in wild populations and captive populations are necessary to strengthen and truly state that the relationships that I have seen with juvenile turtles are transferable to adult turtles in wild populations. My results are suggestive that red-eared slider turtles may negatively impact red-bellied turtles in resource limited environments.

Red-eared slider turtles and red-bellied turtles in a changing climate

During current times it is important to consider the impacts of changing climatic conditions on the maintenance and recovery of native species as well as when considering the establishment of introduced species. In predicting the distribution of a species, habitat availability and environmental conditions are considered (Guisan and Thuiller 2005, Botkin et al. 2007). Environmental conditions considered must include the biophysical conditions within which a species can survive (Porter and Gates 1969). If the environmental conditions are not met then a species will not be found within the region. In terms of global climate change the rapid shift in climate will lead to shifting

distributions of community assemblages and individual species ranges (Williams et al. 2007).

Climate change is likely already impacting the ecological interactions between red-bellied turtles and red-eared slider turtles in Pennsylvania. Increased environmental temperatures lead to warmer water temperatures which influences the activity patterns of turtles by causing shifting patterns in habitat use, thermoregulation and foraging (Spotila et al. 1984, Avery et al. 1993). Warmer environmental conditions will increase the number of interactions that occur between red-bellied turtles and red-eared slider turtles.

In wetlands similar to those at Silver Lake Nature Center, where the diets of these two species were partitioned, increases in species interactions will likely occur early and late in the season as turtles stop/ start brumating earlier/later due to increased water temperatures. The early and late part of the active season for red-bellied turtles and red-eared slider turtles in PA coincides with periods of potential resource limitations due to seasonal vegetative species being senescent.

In wetlands more similar to those at Fort Mifflin, where the diets of red-bellied turtles and red-eared slider turtles overlapped, increased environmental temperatures will lead to increased rates of exploitative competition as the amount of food consumed increases along with increased temperatures. Increased consumption rates may lead to resource limitations of shared dietary species and long term negative consequences for the weaker competitors' population.

Future Research

Population Monitoring

The results presented in this dissertation present the status of the population ecology of red-bellied turtles and red-eared slider turtles in two southeastern Pennsylvania wetland complexes during the study period. If competition occurs between red-bellied turtles and red-eared slider turtles in wild populations then the removal of a significant proportion of the red-eared slider turtle population may have positive effects on the red-bellied turtle populations in the coming years. Red-bellied turtle populations could respond to reduced densities of red-eared slider turtle population decline by increasing growth rates at the individual scale and by increasing recruitment at the population scale. Continued monitoring of red-bellied turtle populations would enable us to determine how the population responds to red-eared slider turtle removals based on measured or calculated growth rates as well as by determining trends in shifting population size. Over the last several years I have marked many individual turtles and through future periodic intensive trapping of these wetlands we could continue to monitor the populations and determine if shifts in red-bellied turtle abundance occur. Positive shifts in red-bellied turtle growth rates or abundances would suggest that red-eared slider turtles do negatively impact wild populations of red-bellied turtles and that red-bellied turtles perform more optimally in the absence of red-eared slider turtles.

A weakness of the research presented in this dissertation is that the comparative research was performed in only two wetlands that differed in wetland characteristics. Expanding the number of intensively studied wetlands to include other large, intact,

species rich wetlands and other small, fragmented, species depauperate wetlands would enable us to determine if the results I obtained at my study sites are replicated on the larger regional scale. Furthermore, if future research included extremely large wetlands with sympatric populations of red-bellied turtles and red-eared slider turtles it may be possible to determine if red-bellied turtles and red-eared slider turtles would partition spatial resources given enough space. To complete such a large scale monitoring effort would necessitate a large collaboration of private and public stakeholders.

Community Ecology

In the appendix of this dissertation the relative abundances and population size estimates for all five common species found within my study sites are presented. In addition to the population level studies, if we better understood the dietary niches of the full community we would also better understand how the red-eared slider interacts with all members of the turtle community. To do this, additional stable isotope analyses could be performed with scute samples from all of the turtle species present in the wetland complexes I studied. The results of a study like this would place the data presented on red-bellied turtles and red-eared slider turtles within the larger framework of community ecology and could determine the ecological role of red-eared slider turtles.

Genetics Studies

Many interesting questions could also be answered through the use of genetics. Genetic testing could be used with red-bellied turtles to better understand dispersal and relatedness between meta-populations. With red-eared slider turtles genetic testing could

determine the region from which red-eared slider turtles originate and may be helpful to determine if the turtles found within a wetland were introduced to the wetland or if they are the result of active breeding between turtles living within the wetland. To perform genetic studies of red-bellied turtles and red-eared slider turtles at Silver Lake Nature Center and Fort Mifflin would involve analyzing already collected blood samples.

Dietary Analyses

Not fully included in this dissertation are the results of dietary component analyses from stomach flushing and fecal sample collections. Preliminary results are presented in chapter 3 when discussing animal matter consumed by red-bellied turtles and red-eared slider turtles. These results will provide more detailed analyses of the dietary composition of both species diets at Fort Mifflin and Silver Lake Nature Center. When this work is complete there will remain several fecal samples that could be used to compare traditional microscopy based analyses and modern genetic based analyses. Using Next Generation Sequencing could be a modern technique that would allow for better taxonomic identification of dietary items from fresh or ethanol preserved fecal samples. A comparison of traditional microscopy methods and modern genetic sequencing methods could drive ecologists to determine dietary items of study organisms in a more rapid and efficient manner.

Conservation Implications

The persistence of red-bellied turtles in Pennsylvania is not certain. In the most recent surveys of the red-bellied turtle historic range red-bellied turtles were present in only 50% of wetlands from which they once occurred (Stone 2010). If this trend continues then red-bellied turtles will continue to be lost from Pennsylvania wetlands and extirpation from Pennsylvania wetlands is a possibility. Alternatively but less likely, red-bellied turtle populations may be increasing across the region as we more stringently protect our wetland habitats. Human development within the Delaware River Basin, Susquehanna River Basin and Potomac River Basins (i.e. red-bellied turtle range within Pennsylvania) continues to fragment the landscape leading to more highly impacted and degraded wetland habits across the region. Along with this continued habitat degradation the added threat of an increasing red-eared slider turtle populations may continue to reduce the regional numbers of red-bellied turtles across Pennsylvania.

In a continually developing world Pennsylvania continues to be developed and wetland habitats are still being irreparably harmed. If society is to prevent the loss of native species it is imperative that we stem the introduction of non-native species, prevent the fragmentation of intact habitats, preserve what habitats remains and strive to improve and re-establish environments that will enable populations of organisms to grow and persist into the future.

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Appendices

Appendix A. Wetland Description

The Wetlands at Fort Mifflin

The wetland complex at Fort Mifflin (FM) is comprised of four different wetlands. These four wetlands are the Delaware River at Fort Mifflin, EMC-10, EMC-11 and the Moat at Fort Mifflin. For this study I considered the Delaware River at Fort Mifflin as the embayment found adjacent to the Moat at Fort Mifflin. Wetlands EMC-10 and EMC-11 are located adjacent to Hog Island Road and the entrance to Fort Mifflin. The Moat is dug impoundment that surrounds the fort. The Moat is divided into an east and a west side by narrow patches of land.

Wetlands at John Heinz National Wildlife Refuge

The wetland complex at the John Heinz National Wildlife Refuge (JHNWR) is extensive and I focused my work in two main locations near the visitor center. I worked in the north end of the impoundment from just south of the boardwalk that crosses the impoundment. The impoundment is managed for waterfowl and water depth is regulated seasonally. The second site was Darby Creek adjacent to the impoundment. Darby Creek at the JHNWR is a tidal creek with daily fluctuation of approximately three meters.

Wetlands at the Silver Lake Nature Center

The wetland complex at the Silver Lake Nature Center (SLNC) is comprised of five different wetlands. These five wetlands were Silver Lake, Mill Creek, Magnolia Lake, the Unconnected Pond and North Mill Creek. Silver Lake was considered all of

Silver Lake from Rt. 13 in the southern end north to where the Lake narrows out and becomes channelized. Mill Creek began at the channel that opened up to Silver Lake and continued north under Lakeland Avenue and dissipated in a narrow shallow channel that led northward. Magnolia Lake on its southeastern shore began at an opening from Mill Creek just north of Lakeland Avenue and was bordered on the south by Lakeland Avenue, on the west by Oxford Valley Road and on the North and East shores by undeveloped parkland. The Unconnected pond was a shallow pond that was along the northern shoreline of Magnolia Lake. Magnolia Lake and the Unconnected Pond were separated by a narrow strip of land. North Mill Creek was the section of creek that flowed into Magnolia Lake from the north ending at the Pennsylvania Turnpike bridge.

Wetland at the Sugar Creek Farm

The wetland at the Sugar Creek Farm (SugarCreek) was a single small farm pond. It is a shallow depression in the landscape and is used periodically as a source of irrigation water. There is very little riparian vegetation found at this site.

Wetlands at the Willow Creek Orchards

The wetland at the Willow Creek Orchard (WCO) is a single impoundment that was created by damming the slow moving Willow Creek which is found running north and south of the impoundment. The impoundment is surrounded by riparian vegetation and is periodically used as a watering hole for livestock such as cattle and swine.

Appendix B. Number of turtles captured by year and wetland.

Year	Wetland	Species				
		<i>Cp</i>	<i>Cs</i>	<i>Pr</i>	<i>So</i>	<i>Ts</i>
2006	SLNC	246	NA	52	111	51
2007	JHNWR	63	4	3	0	7
2008	SLNC	376	116	159	264	87
	FM	146	43	17	47	15
2009	SLNC	145	33	46	34	14
	FM	328	95	75	151	28
	JHNWR	11	0	2	0	4
	Sugartown	8	9	0	0	0
2010	SLNC	220	30	57	161	23
	FM	221	32	27	54	17
	JHNWR	11	1	1	0	1
2011	SLNC	27	0	4	19	2
	WCO	21	5	0	0	0

Appendix C. Trapping effort in individual wetlands

	Wetland Complex	Wetland Name	Wetland Type	Trap Effort	Trap Effort Basking	Trap Effort Total
2006	SLNC	Silver Lake	Lake	247	0	247
		Mill Creek	Creek	82	0	82
		Magnolia Lake	Lake	238	0	238
		Unconnected	Lake	10	0	10
2008	FM	Moat	Lake	240	0	240
		Delaware River	River	44	129	173
	JHNWR	Darby Creek	Creek	252	84	336
	SLNC	Silver Lake	Lake	810	46	856
		Mill Creek	Creek	524	46	570
		Magnolia Lake	Lake	506	36	542
2009	FM	Moat	Lake	423	0	423
		EMC-10	Lake	210	0	210
		EMC-11	Lake	8	0	8
	JHNWR	Impoundment	Lake	1.65	0	1.65
	SLNC	Silver Lake	Lake	116	0	116
		Mill Creek	Creek	40	0	40
		Magnolia Lake	Lake	162	161	323
		Unconnected	Lake	9	0	9
	SugarTown	Farm Pond	Lake	14	0	14
2010	FM	Moat	Lake	173	0	173
		EMC-10	Lake	258	0	258
	JHNWR	Impoundment	Lake	12	0	12
	SLNC	Silver Lake	Lake	260	1	261
		Mill Creek	Creek	61	0	61
		Magnolia Lake	Lake	289	0	289
2011	SLNC	Silver Lake	Lake	60	0	60
		Mill Creek	Creek	1	0	1
	WCO	Farm pond	Lake	31	0	31

Appendix D. Relative abundance of turtle species by wetland complex.

Year	Wetland	Relative Abundance by Species				
		<i>Cp</i>	<i>Cs</i>	<i>Pr</i>	<i>So</i>	<i>Ts</i>
2006	SLNC	0.53	NA	0.11	0.24	0.11
2007	JHNWR	0.82	0.05	0.04	0.00	0.09
2008	SLNC	0.38	0.12	0.16	0.26	0.09
	FM	0.54	0.16	0.06	0.18	0.06
2009	SLNC	0.53	0.12	0.17	0.13	0.05
	FM	0.48	0.14	0.11	0.22	0.04
	JHNWR	0.65	0.00	0.12	0.00	0.24
	Sugartown	0.47	0.53	0.00	0.00	0.00
2010	SLNC	0.45	0.06	0.12	0.33	0.05
	FM	0.63	0.09	0.08	0.15	0.05
	JHNWR	0.79	0.07	0.07	0.00	0.07
2011	SLNC	0.52	0.00	0.08	0.37	0.04
	WCO	0.81	0.19	0.00	0.00	0.00

Appendix E. Relative abundance of turtle species by individual wetlands within a wetland complex.

Year	Wetland Complex	Wetland Name	<i>Pr</i>	<i>Ts</i>	<i>Cp</i>	<i>Cs</i>	<i>So</i>
2006	SLNC	Magnolia Lake	0.04	0.17	0.45	NA	0.34
		Mill Creek	0.14	0.03	0.56	NA	0.28
		Silver Lake	0.13	0.03	0.56	NA	0.27
2007	JHNWR	Darby Creek	0	0.1	0.9	0	0
2008	FM	Moat	0.06	0.06	0.55	0.16	0.17
	SLNC	Magnolia Lake	0.14	0.13	0.33	0.1	0.31
		Mill Creek	0.05	0.05	0.36	0.27	0.28
		N. Mill Creek	0	1	0	0	0
		Silver Lake	0.2	0.05	0.47	0.09	0.19
Unconnected Pond	0	0.25	0.25	0	0.5		
2009	FM	Delaware River	0	0	0	1	0
		EMC-10	0.1	0.1	0.59	0.11	0.1
		EMC-11	0	0	0.38	0.23	0.38
		Moat	0.13	0.02	0.44	0.15	0.26
	JHNWR	Impoundment	0.17	0.17	0.48	0.17	0
	SLNC	Magnolia Lake	0.17	0.04	0.34	0.12	0.34
		Mill Creek	0.1	0.05	0.62	0.05	0.19
		Silver Lake	0.1	0.04	0.51	0.06	0.29
Unconnected Pond		0.08	0.08	0.08	0.17	0.58	
SugarTown Farm	Sugartown Farm	0	0	0.47	0.53	0	
2010	FM	EMC-10	0.08	0.04	0.76	0.09	0.04
		Moat	0.05	0.04	0.57	0.07	0.28
	JHNWR	Impoundment	0.08	0	0.08	0.08	0
	SLNC	Magnolia Lake	0.09	0.04	0.56	0.06	0.25
		Mill Creek	0.09	0.03	0.57	0.05	0.23
Silver Lake	0.11	0.04	0.46	0.05	0.33		
2011	SLNC	Silver Lake	0.06	0.03	0.6	0	0.31
	WCO	Willow Creek Orchard	0	0	0.84	0.16	0

Appendix F. Cormack-Jolly-Seber open model population estimates and density per wetland

Wetland	Species	Population Estimate	Standard Error	Low Estimate	High Estimate	Species Density/Ha
Fort Mifflin	<i>C. picta</i>	647	40	596	763	162
	<i>C. serpentina</i>	211	12	192	240	53
	<i>P. rubriventris</i>	284	51	210	415	71
	<i>S. odoratus</i>	351	40	292	454	88
	<i>T. scripta</i>	96	74	52	1030	24
Silver Lake Nature Center	<i>C. picta</i>	1056	53	968	1179	50
	<i>C. serpentina</i>	871	247	530	1542	41
	<i>P. rubriventris</i>	764	89	619	973	36
	<i>S. odoratus</i>	2300	240	1892	2838	110
	<i>T. scripta</i>	216	23	118	313	10

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Selected Publications and Abstract

Pearson S. H., Avery HW, Kilham SS, Velinsky DJ, Spotila JR (2013) Stable Isotopes of C and N Reveal Habitat Dependent Dietary Overlap between Native and Introduced Turtles *Pseudemys rubriventris* and *Trachemys scripta*. PLoS ONE 8(5): e62891. doi:10.1371/journal.pone.

Pearson S. H. & Avery H.W., (10 August 2012) Competition between IUCN, near-threatened, red-bellied turtles (*Pseudemys rubriventris*) and invasive red-eared slider turtle (*Trachemys scripta elegans*). 7th World Congress of Herpetology, Vancouver, BC, Canada.

Pearson, S. H., Research Links Turtle's Survival to Wetland Size (2012). *Estuary News*, 22, 6.

Funding and Awards

\$25,000: DuPont Clear into the Future Graduate Student Fellowship. Awarded in September 2008.

\$25,000: DuPont Clear into the Future Graduate Student Fellowship. Awarded in September 2007

Poster Award: Best Student Poster Award, 2011 Delaware Estuary Science & Environmental Summit, Jan. 30 – Feb. 2, 2011, Cape May NJ.

