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THE EXPANSION OF A NATIVE GENERALIST SPECIES FOLLOWING COMPETITIVE RELEASE AND HABITAT DEGRADATION

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THE EXPANSION OF A NATIVE GENERALIST SPECIES FOLLOWING COMPETITIVE

RELEASE AND HABITAT DEGRADATION

BY

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RELEASE AND HABITAT DEGRADATION

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ABSTRACT

The understanding of competitive release and a generalist species' ability to exploit an available niche assists in explaining short- and long-term changes in ecological communities. I evaluated the expansion and establishment of a native generalist species, the red-eared slider (*Trachemys scripta elegans*), into a river community studied over a 50-year period (1969-2019). My objective was to analyze the *T. s. elegans* population upon expansion and how the population has been affected by the short- and long-term changes of the ecosystem. The turtle community in the North Fork of the White River, Ozark County, MO, USA faced habitat degradation, harvesting, a record shattering flood resulting in changes to the riparian habitat, and other stressors. I concluded that the *T. s. elegans* population was able to expand their population into a new geographic area following the reduction of competition and increased basking habitat due to nuisance vegetation growth associated with habitat degradation. The short-term effects of flooding further benefited the expanding population of *T. s. elegans* by increasing nesting habitat. Within the 50-year period, the generalist species, *T. s. elegans*, was able to exploit and thrive in a small niche without harming the dominant species, the northern map turtle (*Graptemys geographica*).

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INTRODUCTION

Anthropogenic activity is altering the composition of ecological communities throughout the world via direct and indirect pathways. Harvesting of wildlife is causing the reduction, extirpation, and extinction of native species which can alter interspecific interactions such as competition (Vörösmarty et al., 2010). Land use and land cover change are altering habitat availability, distribution, and quality at the local, regional, and global scales (Parmesan and Yohe, 2003; Parmesan, 2006; Schell et al., 2020). Climate change is causing temperature to increase over time along with changing precipitation patterns. Generalist species have traits that allow them to persist in a wide range of abiotic and biotic conditions, and tend to fare better than specialist species with more specialized habitat and dietary requirements when faced with environmental change (Pounds, Fogden, and Campbell, 1999; Root et al., 2003; Shoo, Williams, and Hero, 2006; Manthey, Fridley, and Peet, 2011).

Some species expand the boundaries of their native distribution in response to modifications to land use and warming temperatures associated with climate change (Root et al., 2003; Roux and McGeoch, 2008). The range expansion of a variety of taxa has been documented globally (Parmesan, 2006) and traits that make species generalists and numerically abundant contribute to their ability to expand their distribution in response to abiotic and biotic alterations to their environment (Roux and McGeoch, 2008). A species-level response determines the degree in which community reorganization occurs following environmental change (Roux and McGeoch, 2008). It is critical to understand the interaction between species and the rapidly changing environment, but few long-term studies with historical data of species distribution and community composition exist.

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Competitive release, when one of two species competing for the same resource disappears, has the potential to allow species to expand their distribution as interspecific competition is reduced. The relationship between competitive release, habitat alterations, and a generalist species' ability to exploit an available niche may assist in explaining short- and long-term changes in ecological communities. Competitive release may occur as a result of harvesting because as the targeted species undergoes population declines, the niche they occupied may open so that other species can exploit that niche (Lister, 1976; Pitt and Nickerson, 2013). Population dynamics determine distribution and abundance of species within a community over time (Espindola, Parra, and Vázquez-Domínguez, 2019) and anthropogenic changes to populations and their habitats can dramatically alter population dynamics and the ecosystem as a whole (Roux and McGeoch, 2008; Sharpe and Chapman, 2014).

Ecosystems are dependent on turtle communities as turtles are major contributors to the ecosystem biomass and provide ecosystem functions and services such as energy flow, nutrient cycling, dispersal of vegetation seeds, and water quality maintenance (Moll and Moll, 2004; Lovich et al., 2018). In recent years, turtle populations face increased threats from climate change, habitat degradation, harvesting for the pet and food trade, disease, and introduced species. As a result, many species have suffered population decline and extinction (Moll and Moll, 2004; Ernst and Lovich, 2009; Jergenson et al., 2014). Understanding how these threats influence turtle populations and community dynamics in both the short- and long-term is essential to protecting ecosystem functions.

As turtle populations decline globally, other factors in specific niches can allow for small communities to increase due to competitive exclusion by generalist species, either native or invasive (Hayes, Turner, and Weidemann, 2018; Espindola, Parra, and Vázquez-Domínguez,

2019). The red-eared slider (*Trachemys scripta elegans*) is a generalist turtle species indigenous to the Mississippi River system in the United States. *Trachemys scripta elegans* occupy most freshwater habitats, but prefer quiet water with soft bottoms and ample basking habitat (Ernst and Lovich, 2009). Basking is essential for *T. s. elegans* to thermoregulate and maintain an optimum body temperature of 28-29 ˚C (Ernst and Lovich, 2009). Atmospheric temperatures must reach over 10 ˚C before individuals bask atmospherically; aquatic basking by floating in vegetation at the water's surface peaks at a water temperature of 31.5 ˚C (Auth, 1975; Crawford, Spotila, and Standora, 1983). *Trachemys scripta elegans* are omnivorous and opportunistically eat aquatic invertebrates, algae, and vegetation (Ernst and Lovich, 2009). Due to their generalist nature and adaptivity, *T. s. elegans* have been introduced globally through the pet trade, captive release, and commercial aquaculture ventures, and have become invasive (Warwick, 1986; Warwick, Steedman, and Holford, 1990; Ernst and Lovich, 2009). In the United States, populations have been observed natively in 16 states and non-natively in 32 states (Ernst and Lovich, 2009; USGS n.d.). The species is recorded expanding their populations to other bodies of water within their native range. Natural (i.e., non-anthropogenic) reasons for movement and expansion can include searches for habitat, food, or mates (Moll and Moll, 2004).

A river turtle community in southern Missouri has been studied periodically over a 50-year period (1969-2019) (Nickerson and Pitt, 2012; Pitt and Nickerson, 2012, 2013, 2014; Pitt et al., 2021). The ecosystem is able to support a diverse turtle community ranging between five to seven different species depending on the year (Pitt and Nickerson, 2012). The predominant species, the northern map turtle (*Graptemys geographica*) has faced abundant challenges to their population. Between the 1969 and 1980 surveys, a massive harvesting event reduced the abundance of *G. geographica* by approximately 50% (Nickerson and Pitt, 2012). The population

of *G. geographica* did not recover until 2007 by which time the turtle community had more generalist species than had previously been recorded (Pitt and Nickerson, 2012). Over the 50-year study, the site was affected by several changes. Since 1980, habitat degradation including algae blooms, siltation, sedimentation, and pollution have occurred due to human activity (Pitt et al., 2021). Land cover change in the riparian zone occurred as a result of a record-shattering flood in 2017 that increased the nesting habitat of turtles (Pitt et al., 2021). I studied the population of *T. s. elegans* as this species was not observed in the study area during early (pre-1980) surveys. The objective of the study was to analyze the *T. s. elegans* population over the 50-year study period and determine how the population has been affected by the short- and long-term changes in the ecosystem.

METHODS

Site description

The river turtle community and habitat in a 4.6 km section of the North Fork of the White River (NFWR), Ozark County, Missouri, USA has been surveyed periodically since a pilot study in 1968 (Nickerson and Pitt, 2012; Pitt and Nickerson, 2012, 2013, 2014; Pitt et al., 2021). The NFWR is a spring-fed, seventh order stream. The 3597 km^2 North Fork watershed is comprised primarily of forest/woodland and grassland/cropland. Deforestation and riparian development within the watershed in the 2000s accounted for calcareous silt and sediment deposits (Pitt and Nickerson, 2012, 2014). Prior to siltation the stream-bed varied through the site with large boulders, exposed limestone, dolomite bedrock, and chert, dolomite, limestone, and sandstone gravel (Nickerson and Mays, 1973). Comprehensive surveys were conducted in 1969, 2004, 2005, 2006, and 2007, and opportunistic surveys were conducted in 1970, 1971, and 1972 (Nickerson and Mays, 1973).

Field surveys

In 2019, I surveyed the *T. s. elegans* population in the 4.6 km section of the NFWR as part of a broader study to evaluate changes in the river turtle community and habitat that have occurred since 1969. I followed the protocol of Nickerson and Pitt (2012), as I sought to compare the data collected in this study to previous survey data and minimize a sampling bias. The survey section was divided into fifty 92-meter stations. At the beginning of each station a marker was placed, and stream width, depth and substrate composition were recorded to quantify habitat composition. In 2019, data collection was conducted between 17 June and 9 August, weather permitting, totaling 390 persons hours. Surveying of the turtle community was conducted by snorkeling paired with mark-recapture techniques. All captured turtles were weighed, measured,

marked, and released in the same locations as captured. Individuals were marked with a small unique identifying number with black or dark red nail polish, in order to not affect predator-related mortality, and a protective clear topcoat to ensure the identifying numbers lasted the entire field season. Sterile passive integrated transponder (PIT) tags (Biomark, Inc., Boise, ID) were administered into the anterior inguinal region parallel to the bridge of the shell of individuals with plastron length greater than 8.6 cm following the protocol of Buhlmann and Tuberville (1998). Prior to tagging, individuals of size were scanned for a previous PIT tag; if untagged, the injection site was disinfected, and sealed with liquid bandage after injection of the tag. All observational features of turtle morphology including species, sex, behavior, location, and any physical damage or scar were recorded during capture.

Statistical analysis

I used R (R Core Development Team, 2012) to preform statistical analyses with $\alpha = 0.05$. I used the Schumacher-Eschmeyer method to estimate the population size of *T. s. elegans* with 95% confidence intervals for viable years (2004-2019; in 1969 no individuals were recorded, in 1980 too few individuals were recaptured to calculate an accurate population estimate using the Schumacher-Eschmeyer method). A standardized population density for each year was estimated by dividing the population estimate by the area of the research section, calculated by multiplying the mean stream width (the distance between banks at each station marker was measured in the field) and the 4.6 km length of the study site. The Chapman and Overton method was used to compare population estimates of years 2004, 2005, 2006, 2007, and 2019. The total number of individuals distributed by plastron length (PL) was visually compared over the six survey years. Respectively, assumptions of normality and equal variance for the PL distribution were tested using the Shapiro-Wilk and Levene analyses. The mean plastron length was compared among all

sampling years (1980, 2004-2007, 2019) using the nonparametric Kruskal Wallis test because the data were non-normal. A binomial test was used to determine if the sex ratio of *T. s. elegans* for which sex was distinguishable by external secondary sexual characteristics differed from the 1:1 (male:female) ratio which was available through distinguishable external secondary sexual characteristics. A chi-squared test of independence was used to determine if the sex ratio of *T. s. elegans* differed between sampling years.

In order to analyze the distribution of *T. s. elegans* throughout the study site, I calculated the total number of individuals recorded in each station, during each study year. The data was visualized through a heat map of the study section of the NFWR using ArcGIS (Esri, Redlands, CA). To evaluate the interspecies distribution, a visualization of the *G. geographica* and *T. s. elegans* distribution in 2019 was created using the percent abundance of respective populations in every station. The total number of individuals found in each station was divided by the respective total number of individuals recorded to determine a percent abundance. Long-term site fidelity was evaluated by calculating the maximum distance between capture locations of turtles captured in 2004-2007 that were recaptured in 2019. The time between captures was recorded and limited to adult individuals with PIT tags from their first capture in 2004-2007.

RESULTS

No *T. s. elegans* were captured or observed in the research section in 1969 (Table 1). In 1980, *T. s. elegans* were captured within the research section, however too few (n = 2) were recaptured to calculate a Schumacher-Eschmeyer population estimate and 95% confidence intervals (Table 1). There was no significant difference between the small populations of *T. s. elegans* documented in 2004 and 2005 (z = 1.52, P = 0.129; Table 1). The *T. s. elegans* population was significantly greater in 2006 than in 2004 (z = 2.68, P = 0.007) and in 2007 than in 2004 (z = 1.96, P = 0.05; Table 1). No significant difference in population size was observed between 2005 and 2006 (z = -0.226, P = 0.822), 2005 and 2007 (z = -0.112, P = 0.912), 2006 and 2007 (z = -0.032, P = 0.975). The *T. s. elegans* population estimate for 2019 was not significantly different from the population estimate for 2005 (z = 1.65, P = 0.099) and 2007 (z = 1.25, P = 0.209), but was significantly greater than the population estimate for 2004 (z = 3.004, P = 0.003) and 2006 (z = 6.77, P< 0.001; Table 1). The community assemblage over the study period has been dominated by *Graptemys geographica* since 1969. After a 50% reduction in the 1980 *G. geographica* population, *T. s. elegans* expanded into the research section and populations of both species gradually increased until 2019 (Table 2). In 2019, *T. s. elegans* was found in greater numbers compared to previous survey years.

The mean ranks of the PL of *T. s. elegans* for which sex was visually distinguishable based upon external diagnostics characteristics was not significantly different among years (U = 10.87, df = 5, P = 0.054) In 2019, hatchlings (PL = 2.1-4.0 cm) and adults (PL = 14.1-22.0) were more abundant than previous years (Figure 1).

Table 1. Schumacher-Eschmeyer population size and corresponding density estimates of red-eared slider (*Trachemys scripta elegans*) in the 4.6km section of the NFWR. Biomass calculation was based upon the mean stream width and total length of research section for each respective year and represents the area in which a single *T. s. elegans* would be found given the estimated population size.

Sampling year	Total individuals captured (n)	Total recaptured individuals (m)	Estimated population size (N)	95% Confidence intervals	Biomass (1 turtle/m^2)
1969	0	0	0	N/A	N/A
1980*	17	2	N/A*	N/A*	N/A*
2004	16	10	21	14.127-44.185	10852
2005	17	3	54	30.184-244.072	4325
2006	32	12	69	41.220-204.372	3388
2007	21	3	70	35.767-1632.562	3319
2019	63	12	219	131.505-646.964	1063

*Population estimates from 1980 are invalid due to too few recaptured individuals; a minimum of 3 recaptures is necessary for estimation, else the lower confidence value is negative

Table 2. Schumacher-Eschmeyer population size of northern map turtle (*Graptemys geographica*) and red-eared slider (*Trachemys scripta elegans*) in the 4.6 km section of the NFWR over the 50-year study period. N (95%CI) = estimated population size with a 95% confidence interval.

Sampling year	*G. geographica* N (95%CI)	*T. s. elegans* N (95% CI)	*G. geographica* data source
1969	274(237-325)	0	Nickerson and Pitt (2012)
1980	139(94-264)	N/A *	Nickerson and Pitt (2012)
2004	143(109-210)	21(14-44)	Pitt and Nickerson (2012)
2005	114(80-198)	54 (30-244)	Pitt and Nickerson (2013)
2006	246(163-500)	69 (41-204)	Pitt and Nickerson (2013)
2007	308(204-621)	70 (36-1633)	Pitt and Nickerson (2013)
2019	453(354-627)	219 (132-647)	Pitt et al. (2021)

*Population estimates from 1980 are invalid due to too few recaptured individuals; a minimum of 3 recaptures is necessary for estimation, else the lower confidence value is negative
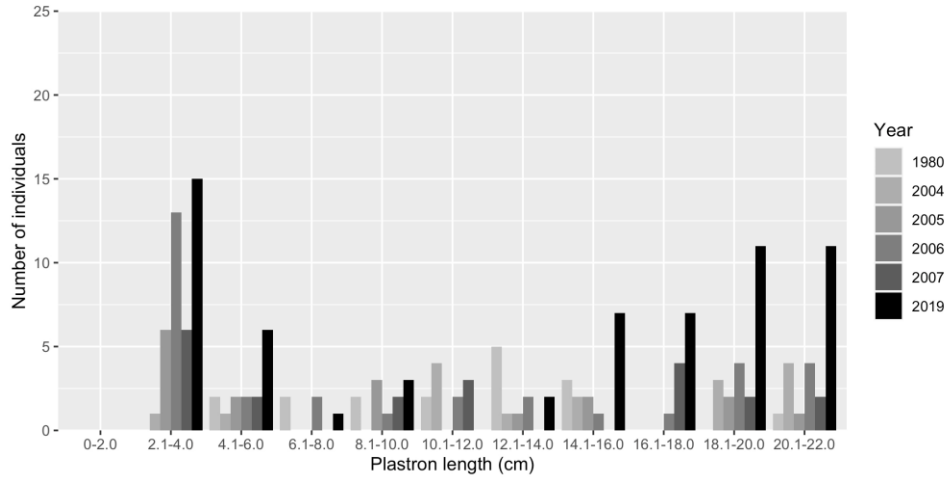
Figure 1. Size distribution based on plastron length of red-eared sliders (*Trachemys scripta elegans*) located in the North Fork of the White River, Ozark County, MO, USA during 1980, 2004-2007, and 2019. Note in 2019 (black bar), *T. s. elegans* had a significantly larger population size than previous years.

The sex ratio for *T. s. elegans* was determined through visually distinguishable external diagnostic characteristics in each respective year (1980, 2004-2007, and 2019; Figure 2). In 2004, 2005, and 2007 the sex ratio was 1 male: 2 females but did not significantly differ from 1:1 ($p_{2004} = 0.15$; $p_{2005} = 0.25$; $p_{2007} = 0.19$; Figure 2). The sex ratio in 2006 was not significantly different from 1:1 (1 male: 1.2 female; $p = 0.4$; Figure 2). The male-biased sex ratios observed in 1980 (1:0.5) and 2019 (1:0.7) were not significantly different from the 1:1 ratio ($p_{1980} = 0.11$; $p_{2019} = 0.21$; Figure 2). There was no significant difference in the sex ratio among years 2004, 2006, and 2019 ($\chi^2 = 2.803$, df = 2, p= 0.246; Figure 2).
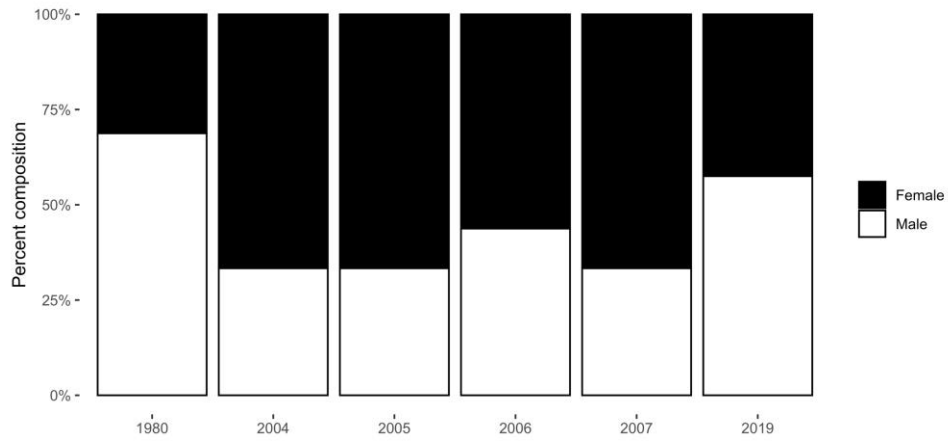
Figure 2. Sex ratio of red-eared slider (*Trachemys scripta elegans*) in 1980, 2004-2007, and 2019 in the North Fork of the White River, Ozark County, MO, USA. Sex was visually distinguishable based upon external secondary sex characteristics.

The distribution of *T. s. elegans* increased throughout the study area from 1980, when they were first observed, through 2019 (Figure 3). The increase in distribution coincided with an increase in abundance of *T. s. elegans* in the study area. In 2004, 16 individuals were found compared to 63 individuals in 2019. Stations 19-24 recorded 48.9 percent of *T. s. elegans* individuals throughout the six years of recorded data (Figure 3).
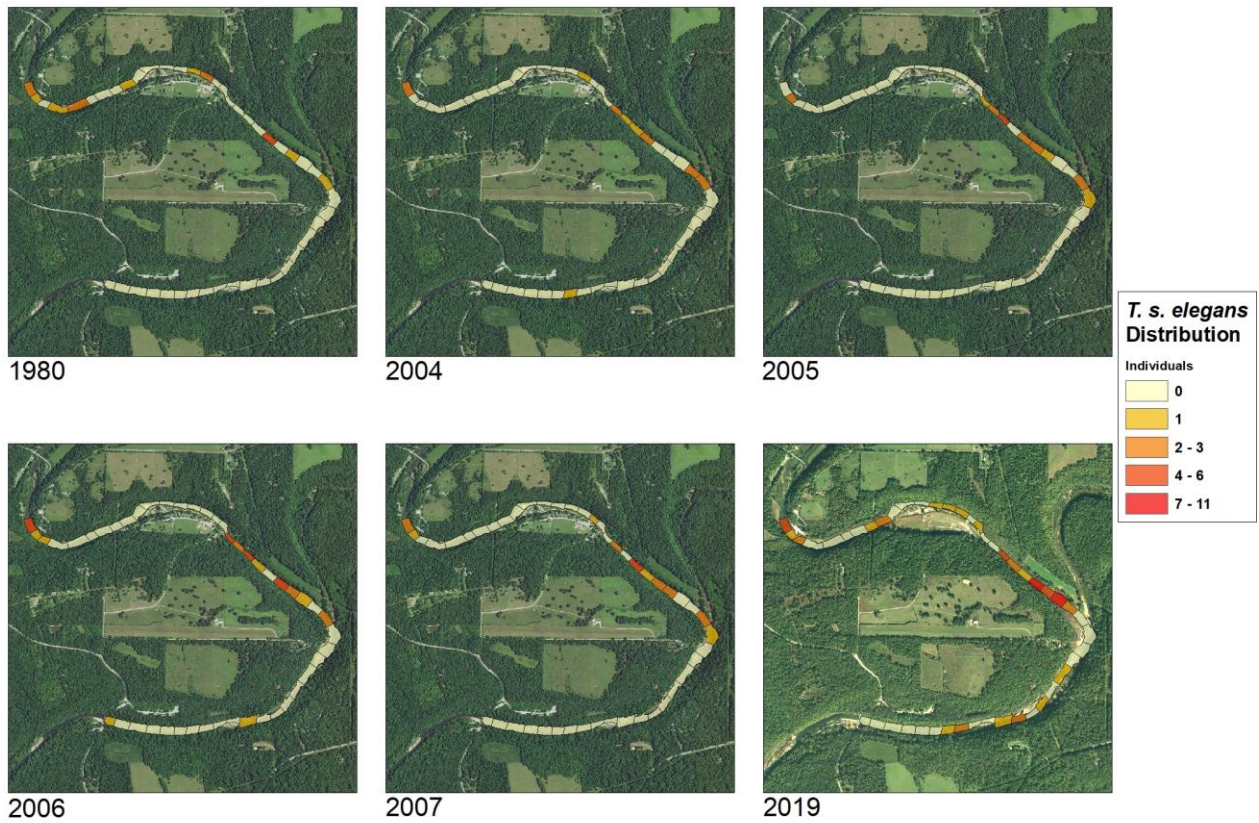
Figure 3. Distribution of the red-eared sliders (*Trachemys scripta elegans*) during recorded years in the 4.6 km section of the North Fork of the White River, Ozark County, MO, USA. Top from left to right: 1980, 2004, 2005; bottom from left to right: 2006, 2007, 2019.

Graptemys geographica had a relatively even distribution throughout the 4.6 km study section compared to the more restricted distribution of *T. s. elegans* (Figure 4). Of the 2019 population of *T. s. elegans*, 60 percent were recorded in stations 19-25 compared to the 26 percent of the *G. geographica* population (Figure 4).

Two female *T. s. elegans* that were captured, and PIT tagged in 2004-2007 were recaptured at least once in 2019. The first female was found 4,735 days apart and traveled upstream by 69 meters from the last capture pre-flood in 2006 and first capture post-flood in 2019. The second female was recaptured 483 meters downstream, 4,355 days from the last capture in 2007 and first capture in 2019.
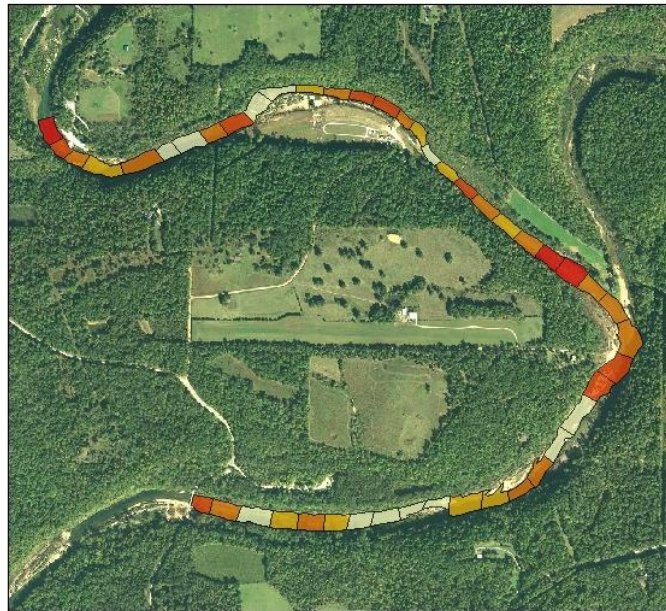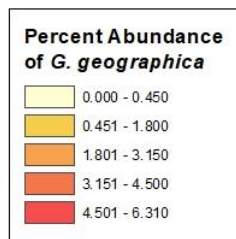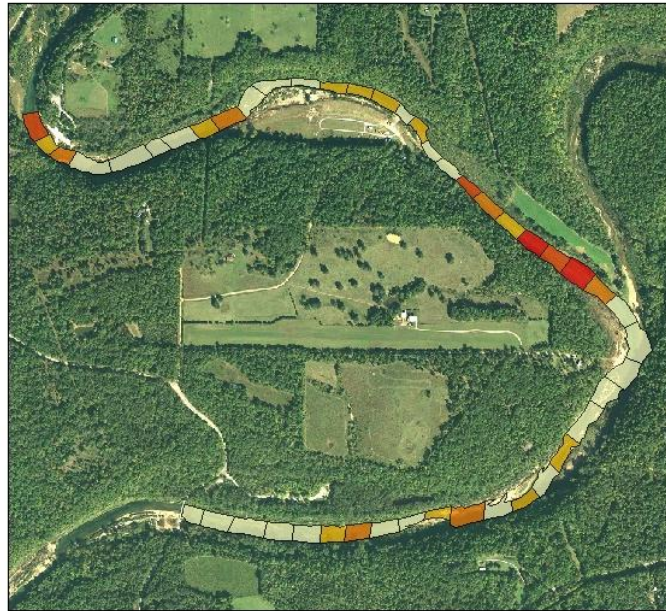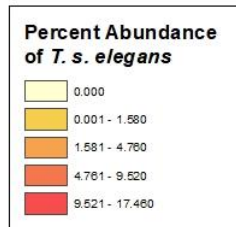
Figure 4. Percent abundance of the 2019 populations of red-eared slider (*Trachemys scripta elegans*) and the northern map turtle (*Graptemys geographica*) in the 4.6 km section of the North Fork of the White River, Ozark County, MO, USA.

DISCUSSION

The progressive increase of the *T. s. elegans* population estimate overtime indicates that once the species expanded its distribution into the research area, the species was able to build a resilient population. *Trachemys scripta elegans* was not observed in the initial 1969 survey but had been observed outside of the research section. By the 1980 survey, a small population of *T. s. elegans* was established within the 4.6 km study section. The appearance of *T. s. elegans* corresponded with a 50% decline of the *G. geographica* population following a mass harvesting event that occurred between 1969 and 1980 (Pitt and Nickerson, 2012). This suggests that the first individuals of *T. s. elegans* were able to exploit an available niche in the study site due to competitive release as the decline of the *G. geographica* population reduced competition for available basking habitat, a critical resource for both species. A generalist species, such as *T. s. elegans*, entering a niche for the first time is at a competitive disadvantage compared to other native species within the range due to access to resources (Cadi and Joly, 2004; Lindsay et al., 2013). Competitive release allowed for the population of *T. s. elegans* to move into and establish within the research section. While sex ratios were not significantly different from 1:1 (male: female), the first *T. s. elegans* population observed in the study area was primarily male dominated (1 male:0.45 females) until the 2004-2007 period when the sex ratio was 1 male:2 females suggesting that either new individuals moved into the area or warmer nesting habitat increasing the female population through temperature-dependent sex determination. *Trachemys scripta elegans* are likely to make overland movements in their lifetime for mates, new aquatic habitat, nesting habitat, or in response to drought (Mali et al., 2016).

While the initial establishment of *T. s. elegans* in the study section was likely enabled by the population decline of *G. geographica*, the increase in the *T. s. elegans* population from 1980

to 2019 indicates the species was thriving during a period of increased habitat degradation (Pitt et al., 2021). Habitat degradation included increased siltation and sedimentation, establishment and spread of nuisance vegetation, and increased water temperatures. Being a generalist species, *T. s. elegans* can survive in subpar habitat by making use of thick vegetation as refugia and aquatic basking habitat, and food (Ernst and Lovich, 2009; Pitt and Nickerson, 2012). The increase in population size between 1980 and 2019 may be due to the expansion of nuisance vegetation into the research section which expanded the niche for *T. s. elegans*. The habitat composition of sections 19-25 of the NFWR included ample basking habitat (down trees, flat basking rocks, and thick vegetation) and no riffles, which is the ideal habitat of *T. s. elegans* (Moll and Moll, 2004; Ernst and Lovich, 2009; USGS n.d.).

After the 2017 extreme flooding event, the population of red-eared sliders was prevalent in the study site indicating the flood did not have negative short-term impacts on the population. The distribution of plastron length in 2019 revealed high numbers of hatchlings and adult *T. s. elegans*, but few juveniles (Figure 1). This indicates two aspects of population distribution in the aftermath of an extreme flood. First, the increase in number of hatchlings is likely due to the increased nesting habitat from the flood. The flood overtook the riparian zone resulting in decreased trees and vegetation on the shoreline (Pitt et al., 2021). Excessive deposits of silt and sand remained within the riparian zone, which is prime habitat for turtle nesting, resulting in a short-term increase in hatchlings. The second result of the flood was the disproportional number of adults recorded in 2019. When exposed to high velocity water, juveniles may have been displaced with the inability to return to the study site due to their size and more limited ability to swim upstream. Tucker, Paukstis, and Janzen (1998) found that displacement due to flooding disproportionately affects generalist species and smaller juveniles. Adult *T. s. elegans*

demonstrate high nesting fidelity and homage when displaced (Tucker et al., 2008), indicating

that they have a desire to maintain their location by avoiding displacement through secure

locations or returning following displacement. The NFWR has karst rock formations that

individuals use for shelter from predators and I suspect they can offer secure locations during an

extreme flooding event (Jergenson et al., 2014; Pitt et al., 2021). The continued monitoring of the

NFWR turtle community is necessary to indicate the long-term effects the flood has on generalist

species like *T. s. elegans* and the turtle community as a whole. Pitt et. al (2021) lists potential

threats to the *G. geographica* population in the NFWR; the *T. s. elegans* populations faces the

same potential long-term threats including presence of new competitors (e.g., Ouachita map

turtles, *Graptemys ouachitensis*) and hatchling predators (e.g., striped bass, *Morone saxitilis*)

now observed in the research section following a dam removal necessitated by flood damage.

The dam removal allowed movement of these new competitors and predators upstream from

Lake Norfork, a large reservoir created by an impoundment in Arkansas. Additionally, reduction

of shading vegetation resulting from flooding could yield higher nest temperature leading to a

female-biased sex ratio associated with temperature-dependent sex determination.

  The results of this study demonstrate that a native generalist species of river turtles is able

to expand their population into a new geographic area following the reduction of a competing

species and maintain a resilient population in conjunction with habitat changes that fosters

nuisance vegetation growth which can serve as aquatic basking habitat and a food source. The

progressively increasing population of the native generalist species, *T. s. elegans*, may have

long-term effects on the native specialist species, *G. geographica*, due to increased competition

for resources. As the area faces increased threats due to climate change, habitat degradation, and

human interference, the changes to the environment may alter competition between the turtle

populations, more studies are necessary to assess the long-term effects.

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