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DETECTION AND OCCURRENCE OF NERODIA HARTERI (SERPENTES: COLUBRIDAE) IN AN UPPER PORTION OF THE BRAZOS RIVER WATERSHED

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DETECTION AND OCCURRENCE OF *NERODIA HARTERI* (SERPENTES: COLUBRIDAE) IN AN UPPER PORTION OF THE BRAZOS RIVER WATERSHED

By

JESSICA RENÉ YATES, Bachelor of Arts

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ABSTRACT

Semiaquatic snakes are disproportionately impacted by habitat alteration adjacent to wetlands because of their reliance on both terrestrial and aquatic habitats. Brazos River Watersnakes, *Nerodia harteri*, are endemic natricines with one of the most restricted geographic ranges in North America. I quantified detection and site occupancy probabilities of *N. harteri* and its sympatric congeners (*N. erythrogaster* and *N. rhombifer*), as well as microhabitat selection within the *Nerodia* community. Within occupied transects, search effort was positively correlated with detecting *N. harteri*, whereas environmental and/or habitat variables were better predictors for detecting the sympatric congeners. Microhabitat selection between the three *Nerodia* species varied, with *N. harteri* selecting for riffle presence and increased canopy cover. The focal species was 97% less likely to be found in habitat characterized by bank vegetation containing saltcedar (*Tamarix* spp.). The results indicate the sympatric *Nerodia* spp. are partitioning their habitat to some degree, likely related to foraging activities. To better understand demographic trends of *Nerodia harteri*, long-term monitoring is needed, and habitat management — such as the preservation of riffle habitat — might be necessary to minimize the risk of continued population declines.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

A fundamental objective of ecology is understanding the factors that affect patterns of biodiversity observed in the environment (Atauri and de Lucio 2001). Biodiversity has declined over the past 50 years, and efforts to slow this loss have been challenging in the face of increased anthropogenic pressures (Butchart et al. 2010; Hoffmann et al. 2010). The main threat to maintaining biodiversity is habitat alteration (Weatherhead and Madsen 2009; Sewell et al. 2012). Fragmentation of a habitat precedes the complete loss of habitat and often produces habitat patches that are analogous to islands (MacArthur and Wilson 1967; Araújo et al. 2006). Populations within those patches are further impacted by processes such as genetic drift which, in turn, can cause the loss of evolutionary potential (i.e., the ability to adapt to changing environmental conditions), and possibly local extinction (Attum et al. 2007; Rodriguez et al. 2012).

Out of the millions of species that are estimated to have existed on Earth, 99% have gone extinct thus far, indicating that extinction is a normal process (Vermeij 1989; Barnosky et al. 2011; Costello et al. 2013; Pimm et al. 2014). This continual loss of species over geologic time is termed the background extinction rate, and is estimated to be approximately one extinction per 10,000 species per 100 years (Ceballos et al. 2010). This rate should be balanced by that of speciation (Barnosky et al. 2011). Exceptions to the background loss of species occur during mass extinction events, when the rate of extinction vastly exceeds the background rate, typically leading to the loss of 70–95% of species (Jablonski 1994; Ceballos et al. 2010). Current extinction rates, ranging from a 50- to 1000-fold increase (but likely underestimated) over the background rate indicate that we are currently in the midst of a sixth mass extinction (Barnosky et al. 2011; Ceballos et al. 2010, 2015). The main processes that appear to play prominent roles in current extinction rates are termed the “evil quartet” — habitat loss, over exploitation, introduced species, and chains of extinction — all of which have anthropogenic origins (Purvis et al. 2000).

Determining what characteristics of a species make it more susceptible to extinction can help guide where conservation efforts are needed most (Todd et al. 2017). Species that are particularly vulnerable generally fall into one of two categories: those with restricted geographic ranges, and those that are large-bodied and sporadically distributed. Species in the first category are often the most imperiled, with the amount of available habitat being the factor that correlates closest with the probability of a species going extinct (Purvis et al. 2000; Manne and Pimm 2001; Jenkins et al. 2015; Todd et al. 2017). The ultimate example of a species that exhibits a restricted geographic range is an endemic species. The proportion of endemic taxa in a given habitat is an important indicator of the overall biodiversity of the region (Dirzo and Raven 2003). Population declines have a proportionately greater impact on endemic taxa than those declines in wider-ranging species, and are typically more accurate indicators of reduced biodiversity (Ceballos and Ehrlich 2002). As such, risk assessment at the population level is becoming a more common management tool among conservation ecologists (Ehrlich and Ehrlich 2013).

Compared to other tetrapods, most species of herpetofauna, and snakes in particular, have received relatively little attention in scientific literature because their cryptic and/or secretive nature poses a challenge for data collection (Greene 1993; Durso et al. 2011). Currently, about 25% of reptiles are considered threatened, although an accurate estimate is likely to be larger (Dirzo and Raven 2003). Population declines among reptiles have occurred at both global and regional scales, but there is a poor understanding of the underlying causes of these declines (Ward et al. 2017). Whereas amphibians have received more attention in the last three decades because of the abrupt losses of species (e.g., Green et al. 2020), reptile species are likely declining at similar rates (Gibbons et al. 2000; Araújo et al. 2006). Patterns of reptile biodiversity typically correlate with temperature and water (McCain 2010), thus rising global temperatures, coupled with associated drought events, could threaten various reptile populations — as documented in past climatic disturbances (Araújo et al. 2006). Because of their reliance on both terrestrial (e.g., hibernacula; Wasser 1985; Costanzo 1989; Greene 1993) and aquatic habitats (e.g., foraging habitat and prey availability; Miller and Mushinsky 1990; Attum et al. 2007; Todd et al. 2017), semi-aquatic reptiles are especially vulnerable to habitat alterations, such as those brought about by drought (Roberts and Lillywhite 1983; Willson et al. 2006; Vogrinc et al. 2018).

In an ecological community, coexistence between species is limited by negative interspecific interactions, such as competition for resources (e.g., habitat and food items; Connor and Simberloff 1979; Gotelli et al. 1997; França and Araújo 2007; Butterfield et al. 2020). Interspecific interactions are especially relevant within communities in which individuals of sympatric species are abundant. The genus *Nerodia* includes several species of semi-aquatic snakes that collectively range across much of North America (Powell et al. 2016). In order for these *Nerodia* spp. to exist syntopically, they should occupy separate niches because limited resources might increase interspecific competition (Hutchinson 1959; Whiting et al. 1998; Roe et al. 2004).

Whereas habitat is typically the most common resource to be partitioned in communities of sympatric species, diet composition is often more reflective of niche partitioning within a community of snakes (Hutchinson 1959; Schoener 1974; Toft 1985). This phenomenon has been documented in communities that include natricines, especially those comprised of sympatric *Nerodia* spp., and is accomplished by either consuming prey of different sizes (Lind 1990; Miller and Mushinsky 1990; Greene 1993; Bowen 2004) or different species, across ontogenetic stages (Williams 1969; Hebrard and Mushinsky 1978; Mushinsky et al. 1982; Luiselli et al. 2007). The distribution of resources (e.g., prey availability) within a habitat directly impacts the way by which snake species partition their diet, and indirectly impacts the way those predators occupy foraging habitat (Manjarrez and Macías García 1991; Perkins 2016; Butterfield et al. 2020). Arita and Rodríguez (2002) reported that the structure of a community can be predicted by analyzing the way by which individuals use specific resources. An endemic species (i.e., one with the most restricted geographic range) that has specific resource requirements, such as diet and/or aquatic microhabitats, would be predicted to be more vulnerable to extinction, both locally and across its range.

The Focal Species

Brazos River Watersnakes, *Nerodia harteri*, are medium-sized natricines (colubrid snakes with a semi-aquatic lifestyle), characterized by a unique pattern of olive-brown blotches (Mecham 1983; Werler and Dixon 2000; Gibbons and Dorcas 2004). The species was first collected in 1938 by Phillip Harter, for whom it is named, along a stretch of the Brazos River in Palo Pinto County, Texas (Trapido 1941), and further populations were documented by Tinkle and Knopf (1964), Smith (1983), and Dorcas and Mendelson (1991). The species was known only from the Brazos River watershed until a similar snake was described by Marr (1944) from the Colorado River watershed, and later proposed as a subspecies, *Nerodia harteri paucimaculata* (Concho River Watersnakes; Tinkle and Conant 1961). These two watersheds are separated by approximately 90 km at their closest distance and because of the snakes' suggested intolerance to desiccation, restricted habitat, and relatively brief life span (2 years; cf. Brown and Weatherhead 1999; Mills 2002; Gibbons and Dorcas 2004), gene flow is thought to be restricted between the watersheds. Because of this, Rose and Selcer (1989) suggested that *N. h. paucimaculata* be elevated to specific status. The elevation to full species was further supported by molecular evidence (Densmore et al. 1992); thus, *Nerodia harteri* is hereinafter restricted to Brazos River Watersnakes.

Nerodia harteri is one of two endemic snake species of Texas, along with *N. paucimaculata* (Werler and Dixon 2000), and has one of the most restricted geographic ranges of any North American snake, occupying roughly 300 km of the Brazos River and some of its tributaries (Wade 1968; Mecham 1983; Rose and Selcer 1989). *Nerodia harteri* has been documented as far upstream as Paint Creek in Throckmorton County and Deadman's Creek in Jones County, and ranges as far downstream as the FM 1118 bridge crossing into Bosque County (Werler and Dixon 2000). This limited geographic range is attributable to the species being found rarely more than 3 m from the water's edge (Scott et al. 1989; Werler and Dixon 2000; Gibbons and Dorcas 2004). When compared to sympatric *Nerodia* spp., *N. harteri* tend to associate with riffle habitats, especially in the juvenile life-history stage (Scott et al. 1989; Densmore et al. 1992; Greene et al. 1994; Roelke and Rains 2014). When out of water, the snakes can most often be found sheltering under large stones that facilitate effective thermoregulation (Scott et al. 1989). The combined preference for riffle habitat and rocky shoreline means that *N. harteri* exhibits relatively strong site fidelity when compared with other snake species encountered in the community (Gibbons and Dorcas 2004; Rodriguez et al. 2012).

Nerodia harteri is a viviparous species, with both sexes typically attaining sexual maturity in their second year. Females produce one litter per year of 7 to 23 offspring, and annual survivorship is low for this species, attributable primarily to overwintering mortality and predation (Conant 1942; Fitch 1999; Werler and Dixon 2000; Gibbons and Dorcas 2004). Because of their limited geographic range, *N. harteri* is listed as near-threatened by the International Union for the Conservation of Nature (IUCN), and threatened in Texas.

The sister taxon, *Nerodia paucimaculata*, was given federal protection in 1986 because of the reduction of suitable habitat and the impending construction of the O.H. Ivie Reservoir, completed in 1990 (Stefferud 1986). At that time, *N. paucimaculata* were intensively studied as part of the federal listing and Greene (1993:104) reported that the snakes were not rapidly declining but instead maintaining “vigorous populations” where habitat was suitable. The species was delisted in 2011 after it was determined that Stefferud’s (1986) data on distribution and abundance were inaccurate (Siekaniec 2011). Scott et al. (1989:385) completed a thorough survey of both *N. harteri* and *N. paucimaculata*, conducting field studies from 1979 to 1987, and suggested that both species were “relatively secure” so long as there was suitable foraging habitat for juveniles, identified as the most important factor constraining the species’ distribution. A low detection rate for the snakes (cf. Rossi and Rossi 1999), combined with the growing water demands of central Texas, led to the State initiating an updated assessment focusing on the range-wide distribution and relative abundance. McBride (2009) determined that whereas the general range of *N. harteri* was intact, the snakes were found at fewer sites overall and, where present, densities had declined, making it a rare snake within the area. Since this second comprehensive survey, concern has been raised again for *N. harteri* because more recent efforts to document the species' occurrence have suggested further population declines and extirpations (Rodriguez et al. 2012; Roelke and Rains 2014; M. Fortsner, pers. comm.).

Threats to *Nerodia harteri*

Like other snakes with specific microhabitat requirements, the most significant anthropogenic threat to *Nerodia harteri* is habitat alteration (Scott et al. 1989; Laurent and Kingsbury 2003; McBride 2009; Stanford et al. 2010; Pike et al. 2011). The Brazos River has experienced extensive alteration of riverine habitat in the form of damming over the last 100 years to meet a growing demand for water (TWDB). This trend is consistent with the rest of the U.S., which contains more than 80,000 dams– half of which were constructed after 1950 (Skalak et al. 2013; Scarpino 2018). Dam construction has fragmented linear river habitats to produce lotic patches that are interrupted by lentic reservoirs. These changes in lotic habitat can lead to disjunct distributions of riverine species and, eventually, the local extinction of populations (Griffen and Drake 2008). Furthermore, those species that are unable to migrate from one suitable habitat patch to another often have reduced fitness (Madsen et al. 1996) and/or be unlikely to recolonize extirpated populations (Dubey et al. 2011). While Williams (1969:29) reported that the futures of *N. harteri* and *N. paucimaculata* (then a single species) were "very bleak," Scott et al. (1989) later documented established populations of *N. harteri* at Possum Kingdom Reservoir (Palo Pinto Co.) and Lake Granbury (Hood Co.). Even though the presence of the species at these two reservoirs along the Brazos River is well-documented

(Scott et al. 1989; McBride 2009; S. Harding, pers. comm.), the effects of altered habitat both up- and down-stream of these impoundments remain to be investigated.

Saltcedar (*Tamarix* spp.) is an introduced species of deciduous tree in the western portion of North America, first used as an ornamental plant and then planted as a bank stabilizer in the late 1800s (Graf 1978). Saltcedar grows well in the high-moisture conditions along the peripheral regions of riparian habitat and, once established, is highly tolerant of disturbances (e.g., drought, fire, and flooding; Natale et al. 2010). It is a long-lived tree that is a dominant competitor over other riparian vegetation and produces many offspring that disperse via water and wind (Di Tomaso 1998; Zavaleta 2000; Sher 2013). *Tamarix* spp. are phreatophytic, capable of establishing both deep tap roots to reach the water table below, and dense, profuse fine lateral roots that exploit water throughout the entire soil profile (Nippert et al. 2010). Saltcedar is a halophyte that secretes salt via glands in its leaves, to which native riparian species are intolerant (Storey and Thomson 1994). Saltcedar has been shown to exacerbate channel-narrowing and increased sedimentation along rivers following dam construction (Brotherson and Field 1987; Friedman et al. 1996, 2005; VanLooy and Martin 2005; Dean and Schmidt 2011). In some areas of the Brazos River, the width of the channel has narrowed by as much as 71% from historic levels, and this effect could have potential impacts on *Nerodia harteri*, such as the loss of foraging habitat (Brotherson and Field 1987; Werler and Dixon 2000). In the southwestern United States, communities of wildlife species inhabiting dense saltcedar stands are different than those of native stands. Mammals exhibit decreased species diversity in dense *Tamarix* thickets (Hink and Ohmart 1984), and several lizard species have benefited from saltcedar removal in New Mexico (Bateman et al. 2008).

The aggressive nature of the introduced species *Solenopsis invicta* (Red Imported Fire Ants), and their lack of natural predators, have been implicated as possible contributors to declines of various herpetofauna (Landers et al. 1980; Allen et al. 1997; Tuberville et al. 2000). Researchers have suggested that *S. invicta* is a possible source of mortality for neonate *Nerodia harteri* (Allen et al. 2004; McBride 2009; Rodriguez et al. 2012). Larger watersnakes have greater physiological endurance than younger conspecifics (Pough 1978), so even if direct mortality of *N. harteri* from attacks by fire ants is rare, the increased physiological stress resulting from increased avoidance behaviors could impact neonate snake health, and therefore survival (cf. Seymour et al. 1987; Hawthorne and Goessling 2020). Indeed, modified behaviors in response to introduced species have been documented in populations of *Nerodia* spp. (King et al. 2006).

Another potential impact on the biology of *Nerodia harteri* is snake fungal disease (SFD), which has been implicated in severe population declines of other snake species (Lorch et al. 2016). The pathology of SFD in snakes includes the development of thickened, necrotic tissue that produces yellow or brown lesions that are conspicuous along multiple scales (Lorch et al. 2016; McKenzie et al. 2018). The causative agent, *Ophidiomyces ophiodiicola,* is generally limited to the epidermis of the organism but, in more severe cases, might invade underlying tissues, leading to the formation of nodules

(Lorch et al. 2016). More advanced cases and clinical symptoms are rare in the wild on account of the animal succumbing to secondary diseases and their effects, such as starvation, impaired vision, and bacterial infections (Lorch et al. 2016; McKenzie et al. 2018). The snake's immune response to an SFD infection produces an increased frequency of ecdysis and, if the infection is limited to the outer epidermal layers, the snake might be able to recover (Lorch et al. 2016; McKenzie et al. 2018). Moist environments could promote the growth of *O. ophiodiicola*, and host species occurring within aquatic habitats might have a higher susceptibility to developing an infection (Lorch et al. 2016). Recent work suggests that *N. harteri* experiences higher rates of SFD infection when compared to syntopic watersnakes (S. Harding, unpublished data).

Objectives

The Texas Parks and Wildlife Department (TPWD) commissioned a survey of *Nerodia harteri*, focusing on both occupancy and detectability of the species and survivorship of individuals within intact riverine habitat, to the exclusion of reservoir populations. This survey was particularly timely in light of on-going human water demands. Since 2007, the Cedar Ridge Reservoir has been proposed as an impoundment along the Clear Fork of the Brazos River that would inundate approximately 55 km of river habitat (McBride 2009). While the past 15 years have not seen any advance of the project, the potential impacts on *N. harteri* could be severe, particularly when combined with other existing factors that threaten the species. Long term monitoring of the species should be continued to distinguish between normal population fluctuations and true population declines or extirpations, as well to determine how much search effort should be expended to declare the species absent from a site (MacKenzie and Royle 2005). The objectives of my thesis research are as follows:

(1) To update the status of *N. harteri* at specific localities where it was historically known to occur.

(2) To provide an estimate of survivorship for the species using recaptures of uniquely-marked individuals.

(3) To determine if certain environmental variables (e.g., temperature, river velocity, number of riffles within a transect, etc.) can predict the detection and occurrence of *Nerodia* spp. For *N. harteri*, within the habitat encompassed by the surveyed localities, I expect to encounter the species at locations having greater availability of in-stream riffle microhabitat for sheltering and/or foraging (when compared to other surveyed locations).

(4) To quantify the microhabitat (e.g., riffle presence, canopy cover, density of saltcedar) utilized by sympatric *Nerodia* spp. and determine if *N. harteri*, given its microhabitat specialization, occurs in association with some snake species (i.e., congeners) more frequently than others (e.g., those outside *Nerodia*) within the community. Rossi and Rossi (1999) cited competition with congenerics as a possible reason for decreased detection rates of *N. harteri*. Certain microhabitat features (e.g., canopy cover, density of saltcedar, etc.) measured when encountering snakes might also correlate with *N. harteri* occurrence, even though such patterns are not known from previous assessments of this species. Should these variables have an identified

relationship with the life-history of *N. harteri*, my thesis will provide a baseline against which future assessments of the species can be compared.

Specific to the last objective, I predict that: (a) in transects where *Nerodia harteri* are present, other natricines such as *N. erythrogaster* and *N. rhombifer* will likely be present as well, but not necessarily utilizing the same microhabitat features (cf. Whiting et al. 1998 for *N. paucimaculata*); and (b) *N. harteri* will not associate with non-natricine snakes as frequently as it does with natricines occurring within the Brazos River watershed.

MATERIALS AND METHODS

Surveys

Based on a comprehensive review of satellite imagery and published localities, I established 15 survey sites (Figure 1) containing representative microhabitat for *Nerodia harteri*: stretches of river that consist of both shallow riffles and shoreline with suitably-sized rocks (≥10 cm in their shortest dimension; McBride 2009). Because transect methods have been shown to be an effective method of surveying low-density, microhabitat specialists (cf. Lacki et al. 1994), I demarcated a 250-m transect at each site that followed the river course. One transect was located on Deadman Creek, 9 transects were located on the Clear Fork of the Brazos River, and the final 5 transects were located on the main branch of the Brazos River, downstream from Possum Kingdom Reservoir.

From 2020-2021, I visited these transects on 4 occasions per year that encompassed the activity season of *Nerodia harteri*, with 2 of those occasions coinciding with periods of high activity (cf. McBride 2009). Each sampling period spanned 5 days and was separated by approximately equal time intervals: Spring (early April to early May), early Summer (June), late Summer (August), and Autumn (early October). As such, each transect was surveyed 8 times over the course of the study. So that search effort could be maximized, the order in which I visited the transects within each sampling period was determined by geographic proximity (thereby minimizing travel time). In portions of the watershed where spacing between transects was relatively close, I varied the visitation order and time of day such that, within a sampling year, I visited every transect at each of three approximately equal periods of the day (morning, mid-day, and afternoon), which minimized temporal bias in sampling effort. The exact time that I initiated a survey varied depending on local weather conditions and the number of snakes captured at prior transects.

During all transect surveys, I was accompanied by 1-3 other people who had experience surveying habitats for snakes. I recorded the start and end time of all transects, as well as the number of people surveying, to quantify search effort (person-hours per sampling event) and catch-per-unit-effort (CPUE). Whether or not snakes were detected, I recorded the following variables, prior to starting each transect: General climatic data (ambient temperature [°C], humidity [%], barometric pressure [mm Hg], etc., as reported by the nearest National Weather Service station), temperature (± 0.1°C) of both exposed and shaded substrate, and stream velocity (± 0.1 m^3/s, as reported by the nearest United States Geological Survey gauging station).

Starting at one end of the transect, I searched for snakes in both the up- and down-stream directions. I recorded all snakes encountered and attempted to catch all nonvenomous species. Captured specimens were released at their collection site after processing. All captured snakes were also swabbed for SFD according to a protocol in place by TPWD (P. Crump, pers. comm.). On account of unforeseen circumstances, the surveys of 6 transects in August 2021 were conducted 2 weeks after the surveys of the other 9 transects were completed for that sampling period.

Because detection of *Nerodia harteri* is likely influenced by other snake species present within the community, I recorded the following variables for each encounter with those snakes (whether captured or not) outside genus *Nerodia*: GPS coordinates, time of day, and subject activity. Because *N. harteri* is likely to associate with other natricines within the community, for any captures of *Nerodia* spp., the above variables were measured along with the following habitat and life-history parameters (Fitch 1987; Dorcas and Willson 2009; Dodd 2016): riffle presence, canopy cover (estimated % cover using a spherical crown densiometer), and microhabitat (e.g., within the stream channel, under a rock, etc.). I also used a medical cautery unit to uniquely mark each watersnake (Winne et al. 2006).

I measured the above variables in all captured *Nerodia harteri* as well as additional natural history data, including snout-vent length (SVL; ± 1.0 mm), tail length (TL; ± 1.0 mm), body mass (± 0.5 g), gut content if present, body scars present, sex, and, if a gravid female, number of embryos present. Unless otherwise stated, morphometric data are reported as mean ± SE (range). For individuals of sufficient size (≥200 mm SVL), I used a 12-gauge needle to inject a passive integrated transponder (PIT tag) subcutaneously, parallel with the body axis (Camper and Dixon 1988; Gibbons and Andrews 2004; Dodd 2016). To prevent PIT tag loss, I applied liquid bandage (e.g., New Skin) to the injection site.

Those habitat data that did not change dramatically over the course of the study (e.g., canopy cover, riffle presence) collected from *Nerodia* capture locations were compared to 10 randomly-selected locations within each transect (using a random number generator). Because of events that occurred during the August 2021 survey effort, the randomly-selected habitat data at 6 transects were collected 2 weeks after the other 9 transects. Because saltcedar establishment alters riverine habitat in ways that might impact snake occurrence (e.g., narrowing of river channels, siltation of stream habitat; Friedman et al. 1996, 2005; VanLooy and Martin 2005; Dean et al. 2011): (a) I estimated the percent density of saltcedar (to the nearest 5%) along each bank, 5 m up- and down-stream from the location of *Nerodia* captures, and (b) I quantified the total density of saltcedar along each transect by estimating the percent density in 10-m increments along the length of the transect on either bank.

As part of the objectives set forth by TPWD, I noted the presence or absence of *Solenopsis invicta* by collecting any encountered fire ants from each transect, and placing them in a microcentrifuge tube containing 95% ethanol to preserve the ants for later identification. To differentiate between *S. invicta* and *S. geminata* (a species of fire ant native to Texas), I used criteria provided by the Hawai'i Ant Lab.

Statistical Analyses

Survivorship of *Nerodia harteri* was calculated using the *marked* package (Laake et al. 2013) in R Statistical Software (R Core Team 2020). Capture-recapture data were represented by a sequence of zeroes (non-captures) and ones (captures), with every position on the binary string representing a sampling event. Using the Cormack-Jolly-Seber (CJS) model, survival (ϕ) was calculated as a naïve estimate. Estimating survivorship as a function of age class or sex was not possible because of low recapture rates. Survival probability was modeled as follows:

$$\phi = [1 + \exp(-\mathrm{X}\beta)]^{-1}$$

where X is the design matrix with the capture history of the i^{th} watersnake at the j^{th} sampling occasion, and β is the vector of parameters (Laake et al. 2013).

I established detection histories of *Nerodia* spp. along surveyed reaches of the Brazos River — with a value of 1 representing the detection of a watersnake and a value of 0 representing a nondetection — and modelled site occupancy (ψ) and detectability (*p*) using the *unmarked* package in R Statistical Software (Fiske and Chandler 2011). This package, which fits a resource-selection probability function based on logistic regression (cf. MacKenzie et al. 2002), follows the idea that species are imperfectly detected. That is, detection of a species is indicative of presence, but nondetection is not indicative of species absence and inferences of false absence might generate erroneous conclusions of resource use (MacKenzie 2006). The *unmarked* package assumes that (a) both site occupancy and detectability are binomial processes occurring simultaneously, (b) occupancy at a site remains constant during the sampling season, and (c) repeated visits at a site are independent. Site occupancy is considered a Bernoulli random variable, defined as follows:

$$z_i \sim Bernoulli\ (\psi_i)$$

where ψ is the probability of a watersnake occupying transect site i, and z_i is the actual state of occurrence. Detection probability is also treated as a Bernoulli random variable, defined as:

$$\frac{y_{ij}}{z_i \sim Bernoulli\ (z_i p_{ij})}$$

where y_{ij} is the observed presence or absence of a watersnake, and p_{ij} is the probability of detection of the j^{th} observation at the i^{th} site (Einoder et al. 2018). The *unmarked* package also allows detection and occupancy to be modeled reflecting certain predictor variables, site covariates (siteCovs) and observation covariates (obsCovs). Site-level variables are not tied to a specific observation and used to predict site occupancy (e.g., the number of riffles present within a transect), whereas values for observation-level variables are recorded at every sampling event and used to predict detection probability (e.g., ambient temperature, river velocity; Fiske and Chandler 2011). I examined candidate models by first defining a global model that included all siteCovs and obsCovs and then used the *dredge* function from the *MuMIn* package in R Statistical Software (Bartoń 2020). This function has been applied to a wide variety of ecological analyses including those focusing on plants (Vicente et al. 2011), arthropods (Stępień et al. 2021), salmonids (Thomas et al. 2015), birds (Oswald et al. 2018), reptiles (Mitchell et al. 2021), and mammals (Phelan 2018). *dredge* performs an automated model selection from which the output is a list of all possible combinations of variables — including a null model (ψ[.], p[.]) — ranked using second-order Akaike information criterion (AIC$_C$; corrected for small sample sizes). Those models with a $\Delta \mathrm{AIC_C}<2$ were considered to be competitive models (Anderson and Burnham 2002; Arnold 2010). I calculated naïve estimates for detectability and site occupancy of each *Nerodia* sp. over the entire study (subsequent surveys were treated as replicates of survey effort at each transect, n = 120 surveys) and for *N. harteri* as a function of transect and of sampling season. The objective of estimating detectability at these different levels of resolution is to help inform future survey efforts that might have greater constraints in space or time.

To assess the microhabitat selected by *Nerodia* spp., I compared values for the habitat variables that did not dramatically change over the course of the study to random-point data using multivariate multiple logistic regression in the base R Statistical Software, modeled as follows for sites without saltcedar:

$$(Y_1,Y_2,Y_3)_{ijk} = logit(\pi) = \beta_0 + \beta_i C_i + \beta_j R_j + \varepsilon_{ijk}$$

where Y_{ijk} is the probability of the k^{th} individual watersnake present within a specific microhabitat (Y_1 = *N. harteri*, Y_2 = *N. erythrogaster*, and Y_3 = *N. rhombifer*), β_0 is the intercept value, C_i is the fixed effect of the i^{th} percent canopy cover, R_j is the fixed effect of the j^{th} riffle presence (j = 0 if no riffle is present and j = 1 if a riffle is present), and ε_{ijk} is the random error with $\varepsilon_{ijk} \sim \mathrm{NID}(0,\sigma^2)$. β_i and β_j are the slopes associated with the fixed effect variables.

For those survey sites containing saltcedar (*Tamarix* spp.), microhabitat selection was modeled as follows:

$$(Y_1,Y_2,Y_3)_{ijkl} = logit(\pi) = \beta_0 + \beta_i C_i + \beta_j R_j + \beta_k S_k + \varepsilon_{ijkl}$$

where Y_{ijkl} is the probability of the l^{th} individual watersnake present within a specific microhabitat (Y_1 = *Nerodia harteri*, Y_2 = *N. erythrogaster*, and Y_3 = *N. rhombifer*), β_0 is the intercept value, C_i is the fixed effect of the i^{th} percent canopy cover, R_j is the fixed effect of the j^{th} riffle presence (j = 0 if no riffle is present and j = 1 if a riffle is present), S_k is the fixed effect of k^{th} percent saltcedar density, and ε_{ijkl} is the random error with ε_{ijkl}~NID$(0,\sigma^2)$. β_i, β_j, and β_k are the slopes associated with the fixed effect variables. Correlation between continuous independent variables was checked using the *PerformanceAnalytics* (Peterson and Carl 2020) and *psych* (Revelle 2021) packages and the assumptions of normality, independence, and equal variance were assessed visually using the residuals plot generated by the *mvabund* package in R Statistical Software (Wang et al. 2021). Predictions of the response variables for both models were calculated using the *ggiraphExtra* package within in the R platform (Moon 2020).

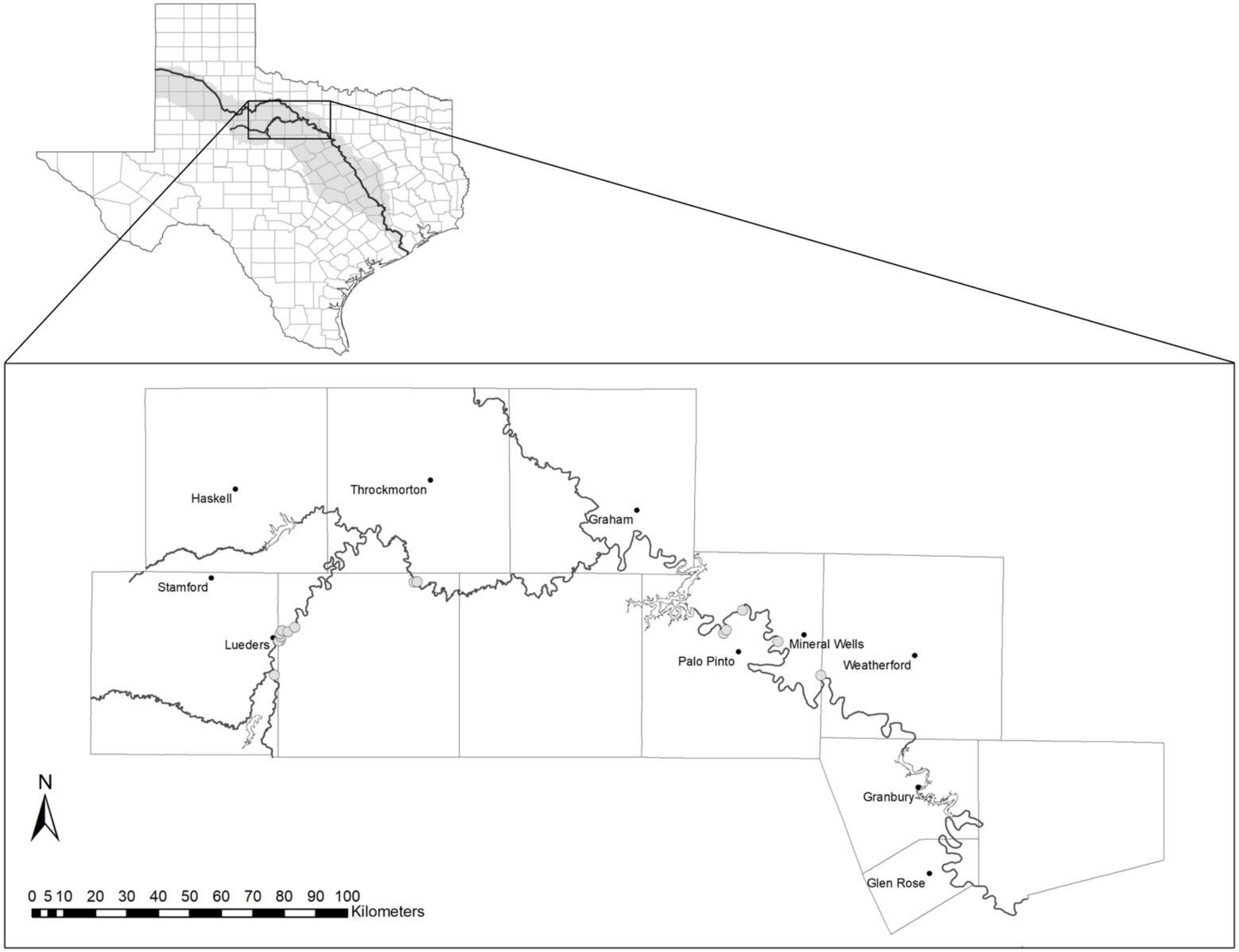

Figure 1A: Map of the Brazos River in Texas (shaded area of inset indicates watershed) with 15 transect locations (shaded circles) surveyed for Brazos River Watersnakes (*Nerodia harteri*).

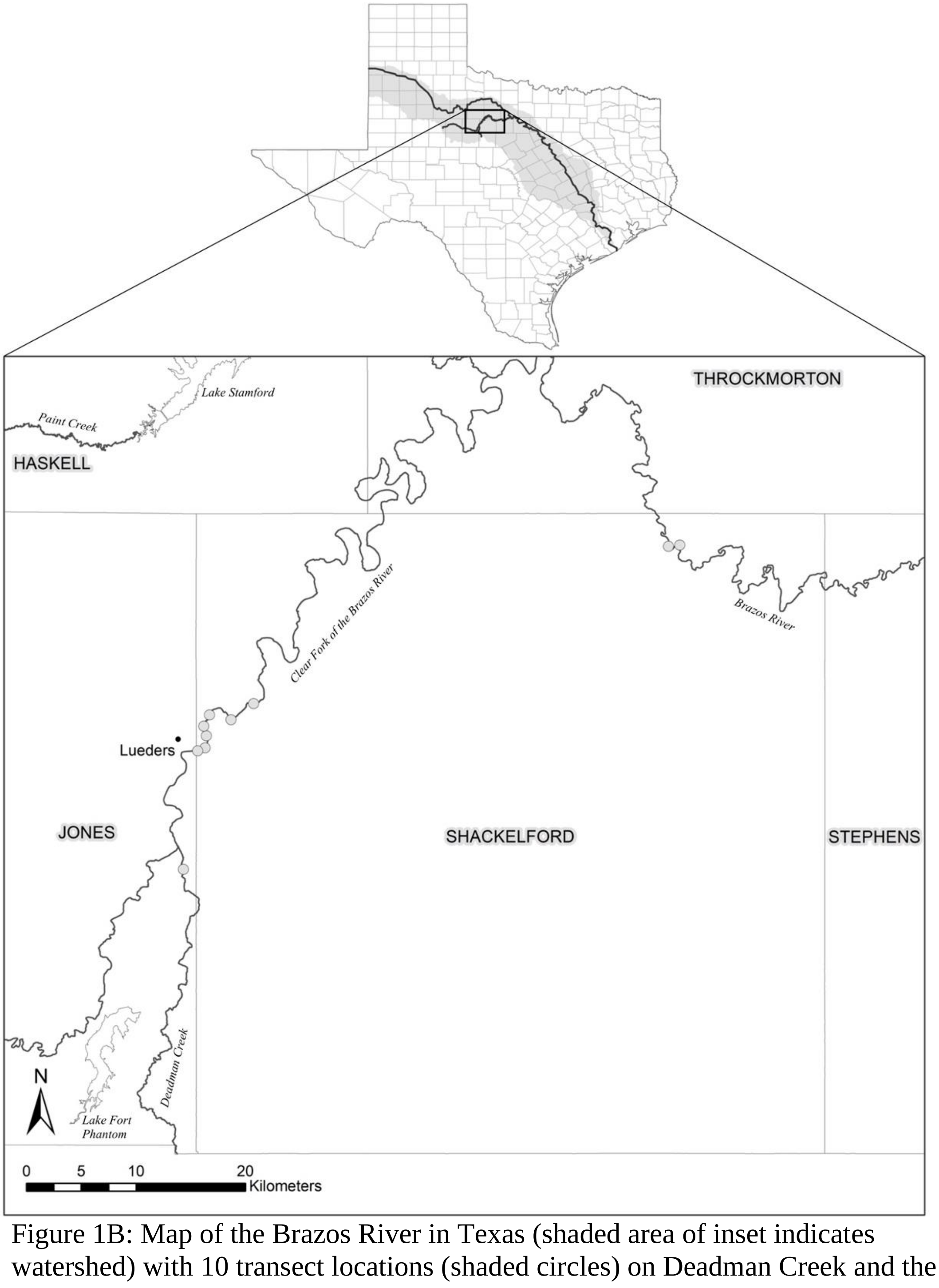

Figure 1B: Map of the Brazos River in Texas (shaded area of inset indicates watershed) with 10 transect locations (shaded circles) on Deadman Creek and the Clear Fork of the Brazos River surveyed for Brazos River Watersnakes (*Nerodia harteri*).

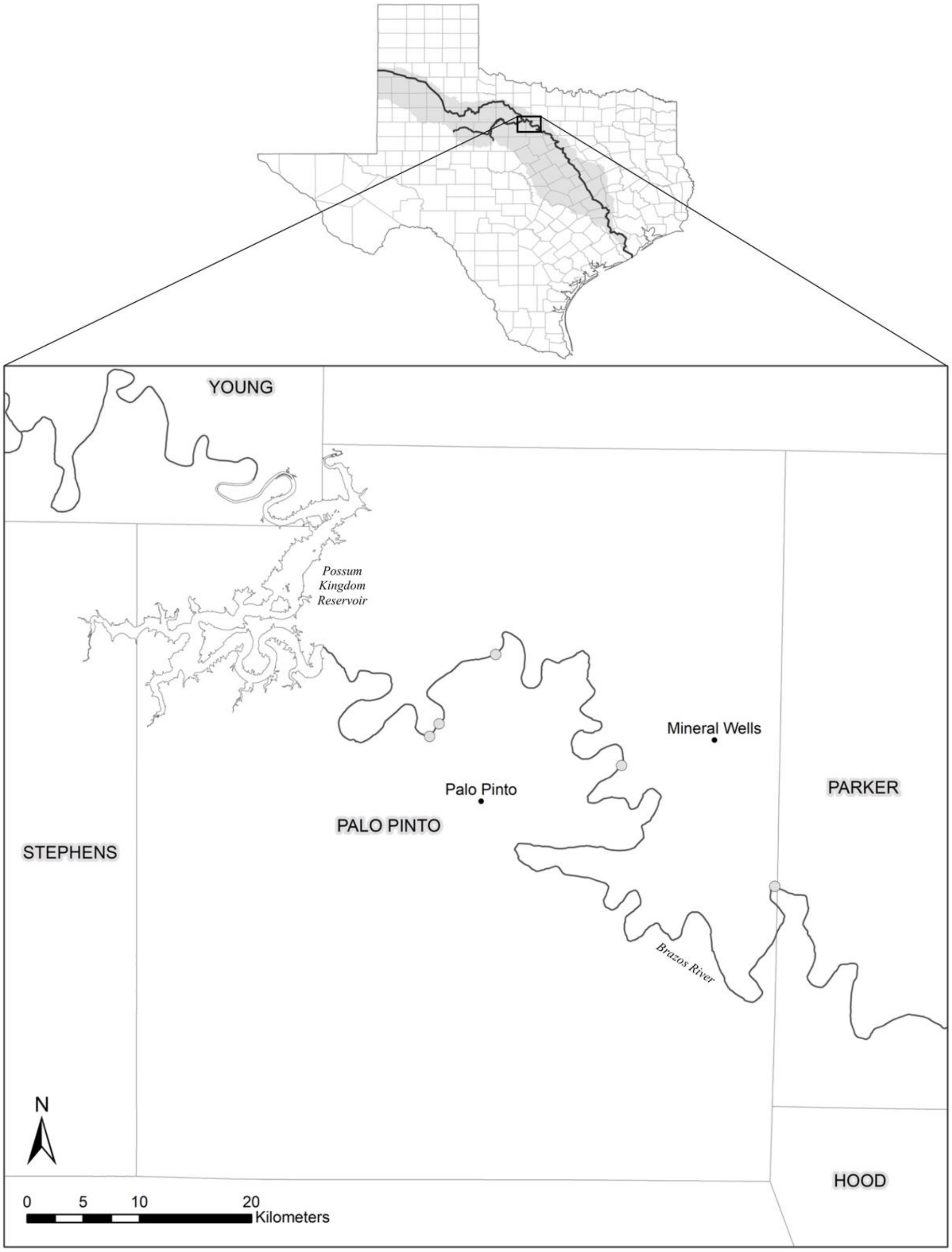

Figure 1C: Map of the Brazos River in Texas (shaded area of inset indicates watershed) with five transect locations (shaded circles) on the Brazos River downstream of Possum Kingdom Reservoir surveyed for Brazos River Watersnakes (*Nerodia harteri*).

RESULTS

Over the course of 292.6 person-hours representing 120 surveys, a total of 188 snakes were observed with 183 of those individuals assigned to 10 different species (see Table A-1 in Appendix). Across all transects, values for total individual abundance and frequency of occurrence were greatest for *Nerodia rhombifer*, followed by *Thamnophis proximus* (29.3% and 27.7% of total observations, respectively). *Nerodia harteri* was the third most abundant species, with observed individuals found in a variety of microhabitats (Table 1). Thirty-six *N. harteri* were observed within 8 of the 15 surveyed transects (CPUE = 1 *N. harteri*/8.13 person-hours), all of which are sited upstream of Possum Kingdom Reservoir. Six additional individuals were observed while canoeing between adjacent, occupied transects. One juvenile *N. harteri* was recaptured in 2021, having been previously caught as a neonate in 2020, within the same 10-m section of a riffle.

All life-history stages were represented among the 31 *Nerodia harteri* captured during surveys (30 individuals, with 1 recapture; Table 2). Eighteen young-of-year snakes were captured, and had a SVL of 221.9 ± 8.5 mm (156.0-273.0 mm), TL of 71.3 ± 2.8 mm (52.0-91.0 mm), and mass of 9.7 ± 0.9 g (3.2-16.0 g). Eight subadults (individuals that have over-wintered once but have not yet reached sexual maturity) were captured, and had a SVL of 321.6 ± 31.1 mm (206.0-451.0 mm), TL of 92.9 ± 11.2 mm (35.0-120.0 mm), and mass of 29.6 ± 7.4 g (7.5-67.0 g). Five adults were captured, and had a SVL of 553.4 ± 27.1 mm (578.0-582.0 mm), TL of 162.6 ± 7.8 mm (136.0-184.0 mm), and mass of 130.0 ± 29.7 g (71.0-228.0 g). Survivorship (ϕ[.]) of *N. harteri* was estimated to be 9.18 ± 62.10%.

Competitive models for occupancy and detectability varied by species (Table 3). For *Nerodia harteri*, search effort was the most competitive model (Figure 2), followed by the null model, and finally a model combining search effort and wind velocity. While not a competitive model for *N. harteri*, increased values in the average density of saltcedar per transect were associated with decreased occupancy probability for this watersnake species (Figure 3). Competitive models for occupancy and detection probability of *N. erythrogaster* included the predictors of the number of riffles per transect and percent humidity, whereas the number of riffles per transect, ambient temperature, and wind velocity were important in predicting *N. rhombifer* occupancy and detectability.

Naïve estimates of occupancy and detection probabilities also varied by species (Figure 4). The probabilities of a site being occupied by either *Nerodia harteri*, *N. erythrogaster*, or *N. rhombifer* were 0.488 ± 0.136, 0.625 ± 0.164, and 0.744 ± 0.145, respectively. The probabilities of detecting either *N. harteri*, *N. erythrogaster*, or *N. rhombifer* were 0.325 ± 0.067, 0.213 ± 0.060, and 0.246 ± 0.055, respectively. Occupancy and detection probabilities for *N. harteri* varied by season with Autumn having a higher detection probability ($p = 0.456 \pm 0.144$; compared to $p = 0.398 \pm 0.120$ for Spring), but lower probability of site occupancy ($\psi = 0.292 \pm 0.129$; compared to $\psi =$

0.460 ± 0.156 for Spring). Detection probabilities for individual sites occupied by *N. harteri* ranged from 0.125 ± 0.117 to 0.750 ± 0.153.

Microhabitats selected by *Nerodia* spp. differed in sites with and without saltcedar. For transects without saltcedar, riffle presence was the most important microhabitat feature predicting the presence of all three *Nerodia* species (Table 4; Figure 5). *Nerodia harteri* were 8.08 times more likely to be found within riffle microhabitats, while *N. erythrogaster* were 15.8 times more likely to be found within riffle microhabitat. *Nerodia rhombifer* were 86.2% less likely to be found within a riffle microhabitat. For *N. erythrogaster* and *N. rhombifer*, percent canopy cover was not a reliable predictor of snake presence. Nevertheless, increases in bank canopy cover were associated with both species being approximately 1.0% less likely to be found. Canopy cover was a moderate predictor for *N. harteri* presence, with the species being 3.0% more likely to be present within microhabitats characterized by increased canopy closure.

For transects with saltcedar, none of the measured microhabitat features were reliable predictors of snake presence for *Nerodia erythrogaster* and *N. rhombifer,* but the selection trends were consistent with those sites lacking saltcedar (Table 5; Figure 6). Percent canopy cover and riffle presence were both significant predictors for *N. harteri* presence, with the species being 4.0% and 35.33 times more likely to be found within those microhabitat features, respectively. While saltcedar was not a significant predictor of snake presence for any *Nerodia* spp., both *N. erythrogaster* and *N. harteri* showed a negative relationship with increased saltcedar density. Specifically*, N. erythrogaster* and

N. harteri were 4.4% and 96.9% less likely to be found in microhabitats characterized by increased saltcedar density along the banks, respectively. *Nerodia rhombifer* had a slight positive relationship with saltcedar and was 6.0% more likely to be found in microhabitats consisting of increased saltcedar density. Pseudo R^2 values for *N. harteri* microhabitat selection in sites with (0.35) and without (0.21) saltcedar were higher than those of their congeners, indicating that *N. harteri* models explained more of the variance.

Table 1: Microhabitats in which *Nerodia harteri* were observed along surveyed reaches of the Brazos River in Texas in 2020 and 2021.

Microhabitat	No. of individuals observed
Rock/debris (sheltered)	23
Rock/debris (basking)	9
Riffle	6
Run/pool	4

Table 2: Morphometric data (mean ± 1 SE) by age class and sex for *Nerodia harteri* captured during surveys of the Brazos River in Texas.

			Morphometric Means		
Sex	Life-history stage	No. of individuals	SVL (mm)	TL (mm)	Mass (g)
Male	Neonate	4	220.5 ± 22.0	78.0 ± 6.9	8.8 ± 2.1
	Juvenile	4	275.8 ± 35.0	92.5 ± 14.2	18.2 ± 6.0
	Adult	2	493.5 ± 28.5	166.0 ± 3.0	81.0 ± 10.0
Female	Neonate	14	222.4 ± 9.4	69.4 ± 3.0	10.0 ± 1.0
	Juveniles	4	367.5 ± 43.6	93.3 ± 19.7	41.0 ± 11.7
	Adult	3	593.3 ± 13.4	160.3 ± 13.9	162.7 ± 39.7

Table 3: Competitive site occupancy (ψ) and detection probability (*p*) models ($\Delta AIC_C<2$) for *Nerodia harteri*, *N. erythrogaster*, and *N. rhombifer*. Occupancy and detection probabilities were either fixed (.) or varied as a function of site and/or observation covariates. Models are ranked according to their AIC_C (second-order Akaike information criterion, corrected for small sample sizes) score and weight (ω).

Model by species	K	AIC_C	ΔAIC_C	ω
Nerodia harteri				
ψ(.), *p*(Person-hours)	3	96.2	0.00	0.197
ψ(.), *p*(.)	2	96.9	0.76	0.135
ψ(.), *p*(Person-hours + Wind velocity)	4	97.9	1.77	0.081
Nerodia erythrogaster				
ψ(No. riffles per transect), *p*(Humidity)	4	91.9	0.00	0.243
ψ(No. riffles per transect), *p*(.)	3	92.8	0.85	0.159
ψ(.), *p*(Humidity)	3	93.8	1.93	0.093
Nerodia rhombifer				
ψ(No. riffles per transect), *p*(.)	3	111.5	0.00	0.255
ψ(No. riffles per transect), *p*(Ambient temperature)	4	112.6	1.12	0.146
ψ(No. riffles per transect), *p*(Wind velocity)	4	113.4	1.90	0.099

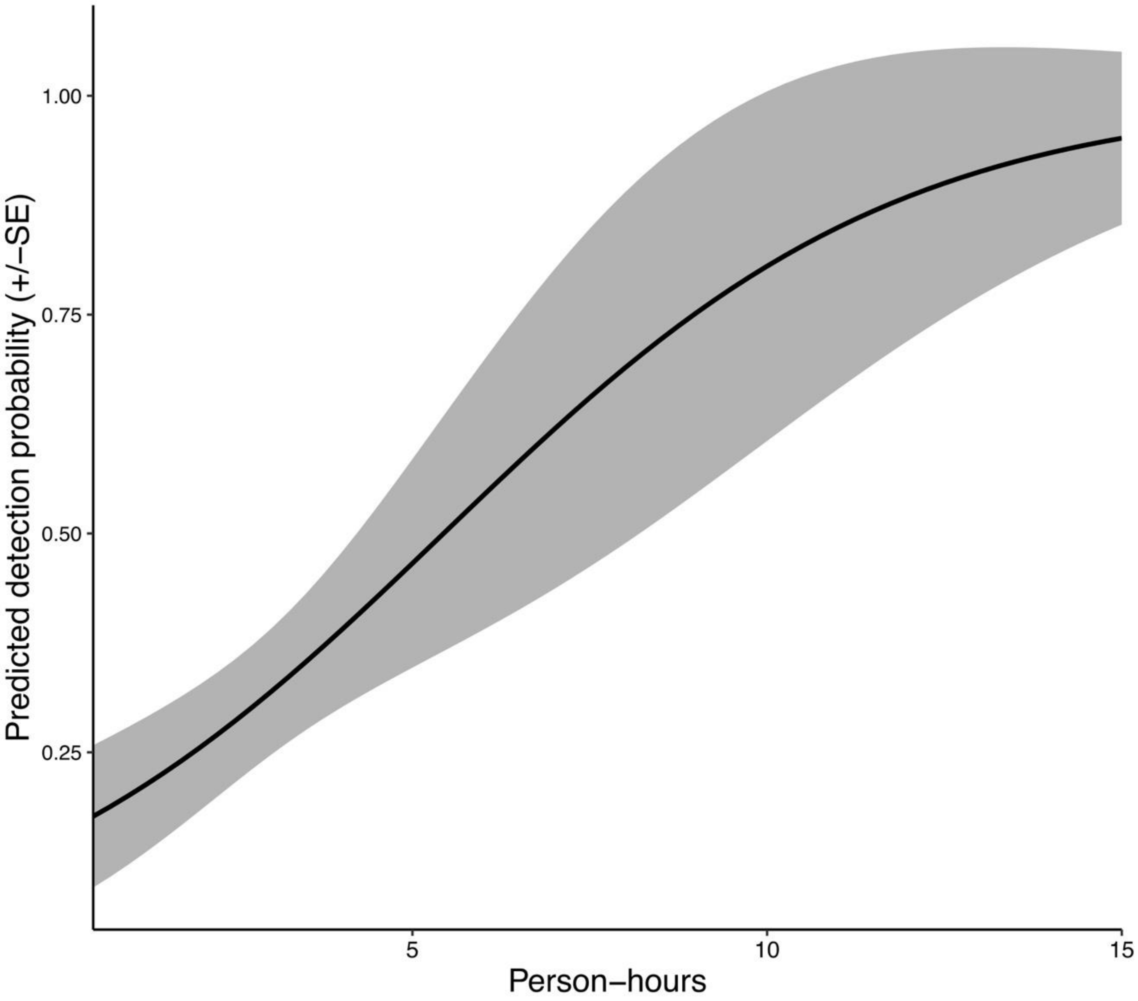

Figure 2: Predicted detection probability (*p*) for *Nerodia harteri* in surveyed reaches of the Brazos River, Texas, as a function of search effort. Gray ribbon represents ± 1 SE.

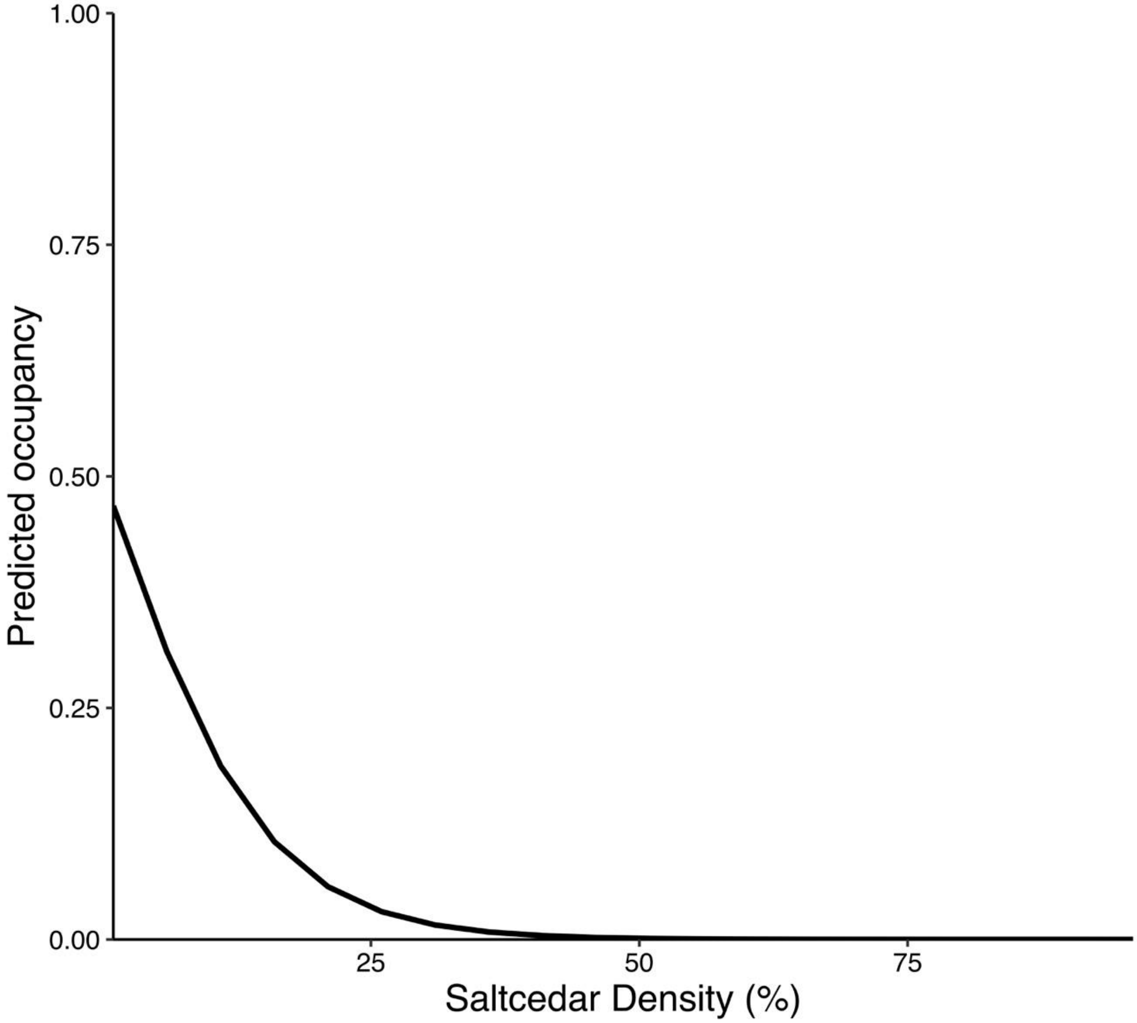

Figure 3: Predicted site occupancy (ψ) probability for *Nerodia harteri* within surveyed reaches of the Brazos River, Texas, as a function of increased average percent saltcedar (*Tamarix* spp.) density.

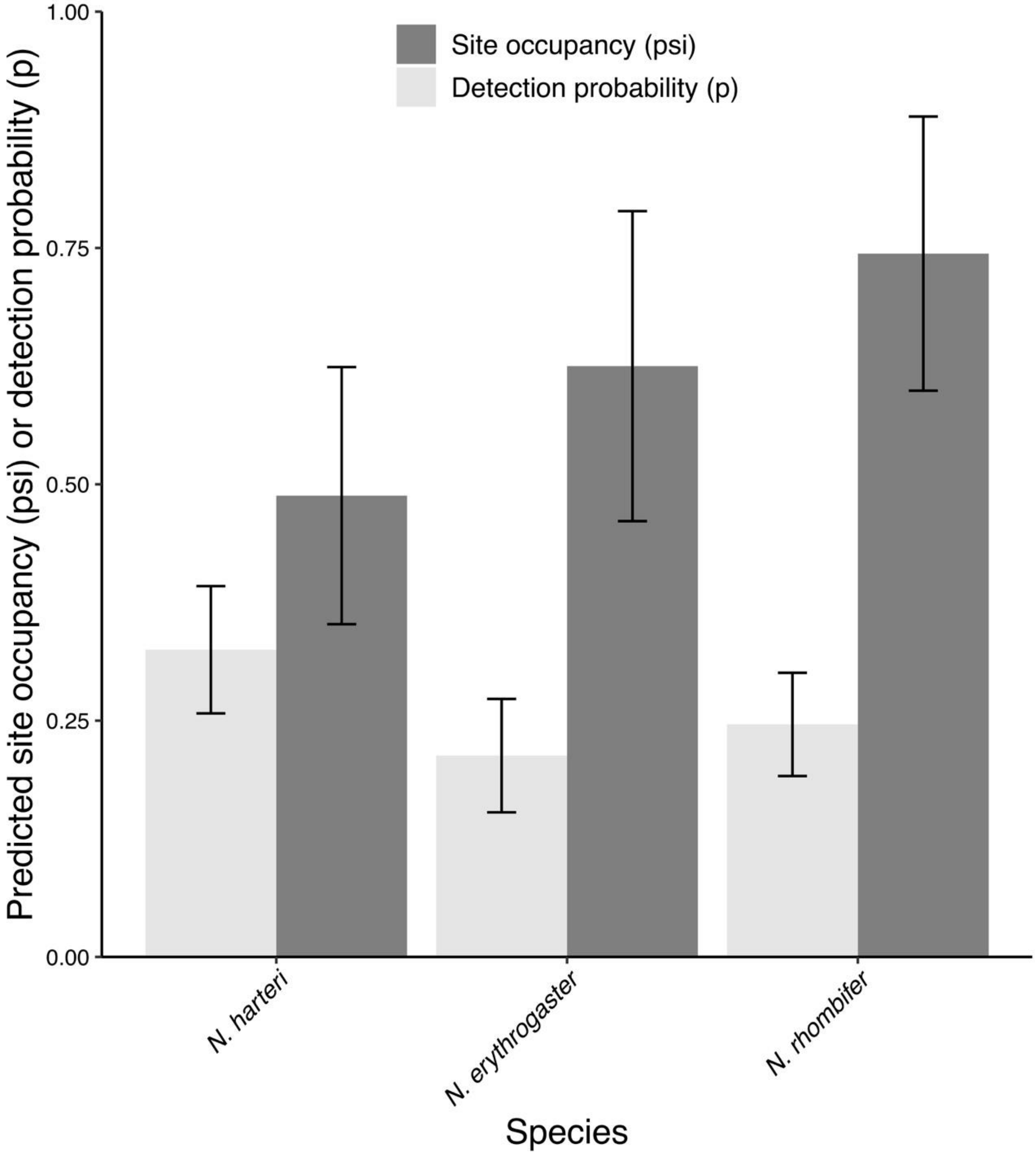

Figure 4: Naïve estimates of site occupancy (ψ) and detection probabilities (*p*) for *Nerodia harteri*, *N. erythrogaster*, and *N. rhombifer* across sampled transects along the Brazos River in Texas. Bars represent ± 1 SE.

Table 4: Logistic regression results for the modeled likelihood of microhabitat selection in *Nerodia harteri*, *N. erythrogaster*, and *N. rhombifer* within those reaches of the Brazos River, Texas, that do not have established saltcedar (*Tamarix* spp.).

Variable by species	β (Estimate)	SE	z-value	p-value	e^{β} (Odds Ratio)	Pseudo R^2
Nerodia harteri						
Intercept	-4.359	0.776	-5.615	<0.001	NA	0.352
Canopy Cover	0.025	0.008	3.228	0.001	1.026	
Riffle Presence	2.089	0.548	3.810	<0.001	8.078	
Nerodia erythrogaster						
Intercept	-4.166	1.131	-3.683	<0.001	NA	0.108
Canopy Cover	-0.001	0.008	-0.075	0.941	0.999	
Riffle Presence	2.760	1.054	2.618	0.009	15.797	
Nerodia rhombifer						
Intercept	-0.819	0.645	-1.270	0.204	NA	0.113
Canopy Cover	-0.014	0.010	-1.404	0.160	0.987	
Riffle Presence	-1.979	0.806	-2.452	0.014	0.138	

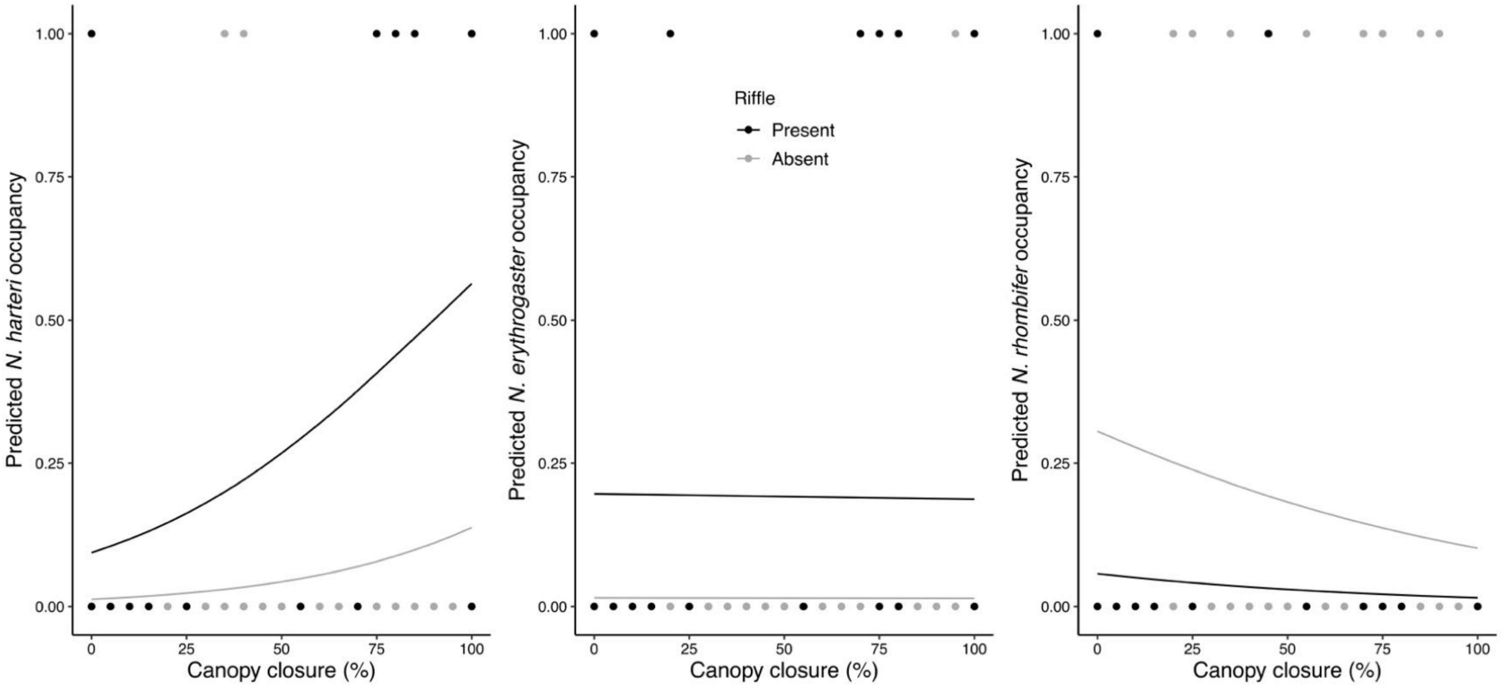

Figure 5: Predicted occupancy for *Nerodia harteri*, *N. erythrogaster*, and *N. rhombifer* as a function of canopy closure within those surveyed reaches of the Brazos River, Texas, that do not have saltcedar (*Tamarix* spp.) established.

Table 5: Logistic regression results for the modeled likelihood microhabitat selection in *Nerodia harteri*, *N. erythrogaster*, and *N. rhombifer* within those reaches of the Brazos River, Texas, that have saltcedar (*Tamarix* spp.) established.

Variable	β (Estimate)	SE	z-value	p-value	e^{β} (Odds Ratio)	Pseudo R^2
Nerodia harteri						
Intercept	-5.403	2.037	-2.652	0.008	NA	0.210
Canopy Cover	0.043	0.022	1.997	0.046	1.044	
Riffle Presence	3.565	1.902	1.874	0.061	35.329	
Saltcedar Density	-3.458	610.676	-0.006	0.996	0.032	
Nerodia erythrogaster						
Intercept	-1.525	1.073	-1.421	0.155	NA	0.149
Canopy Cover	-0.020	0.018	-1.110	0.267	0.980	
Riffle Presence	0.308	1.239	0.248	0.804	1.360	
Saltcedar Density	-0.045	0.116	-0.386	0.699	0.956	
Nerodia rhombifer						
Intercept	-1.283	0.987	-1.299	0.194	NA	0.111
Canopy Cover	-0.018	0.015	-1.223	0.221	0.982	
Riffle Presence	-0.947	1.360	-0.696	0.486	0.388	
Saltcedar Density	0.058	0.044	1.327	0.184	1.060	

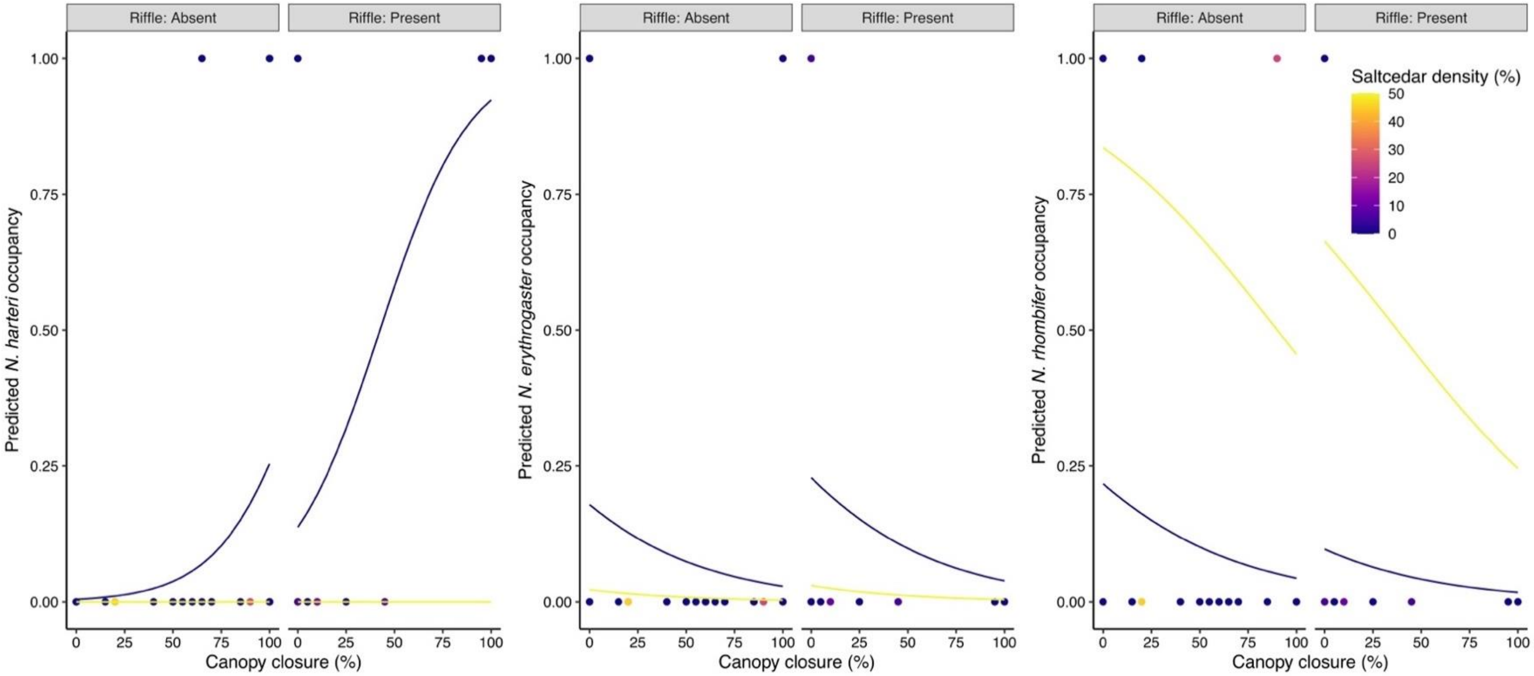

Figure 6: Predicted occupancy for *Nerodia harteri*, *N. erythrogaster*, and *N. rhombifer* as a function of canopy closure within those surveyed reaches of the Brazos River, Texas, that have saltcedar (*Tamarix* spp.) established.

DISCUSSION

Whereas the total number of *Nerodia harteri* observed during my surveys in 2020-2021 was similar to that reported by McBride (2009), the total distance of the river that I surveyed was shorter. In fact, all of my observations of *N. harteri* occurred within transects sited along the Clear Fork of the Brazos River (i.e., upstream of Possum Kingdom Reservoir). Transect locations downstream of Possum Kingdom Reservoir that were reported to be occupied by McBride (2009) and Scott et al. (1989) now seem to be unoccupied. Whereas no *N. harteri* were observed during my surveys of those downstream transects, I did encounter this species in this portion of the Brazos River during a recreational float trip. The individuals observed were found sporadically among riffle habitat, and in low abundance. The pattern of site occupancy revealed during transect surveys could be a result of insufficient search effort and/or poor site selection of transects, but it might also be consistent with population declines reported for the species since the late 1990s (M. Forstner and N. Rains, pers. comm.). So long as appropriate habitat was available (i.e., in-stream riffles and rocky shorelines), healthy populations of *N. harteri* were historically common in portions of the Brazos River downstream from the Possum Kingdom Reservoir (Scott et al. 1989; McBride 2009). This section of river now seems to be occupied disjunct groups of individuals only (pers. obs.; N. Rains, pers. comm.).

The Clear Fork of the Brazos River appears to be occupied by more *N. harteri* populations that are comprised of greater numbers of individuals than those populations downstream of Possum Kingdom. These snakes are part of a breeding population, as exhibited by the large number of neonate individuals that I found in both sampling years — an often underrepresented age class in snake surveys (Ford and Burghardt 1993; Reinert 1993). McBride (2009) noted the lack of neonate snakes found during his survey and suggested a possible population contraction. The continued decline in numbers of individuals reported by authors since then supports this suggestion (e.g., Roelke and Rains 2014). During a 1984 survey of the type locality, 36 individual *N. harteri* were found within 3 person-hours of search effort (N. Scott, Jr., unpublished data). When this site was surveyed by McBride (2009) and myself approximately 4 and 7 times as intensely, respectively, no *N. harteri* individuals were observed.

The continued declines in *Nerodia harteri* populations, long after construction of Possum Kingdom Reservoir (1941; Brazos River Authority), could be a result of long-term habitat alteration caused by impoundments along of the river (Petts 1980). Indeed, long-term population changes and/or declines following river impoundment have been documented in several fish communities (e.g., Quinn and Kwak 2003; Milbrink et al. 2011; Perkin and Bonner 2011). If the alteration of river habitat brought about by the establishment of the Possum King Reservoir is linked to population declines in *N. harteri*, the potential construction of Cedar Ridge Reservoir along the Clear Fork of the Brazos River could mirror these effects on the snakes in the future. Populations of *N.*

harteri have previously been documented along the stretch of approximately 55 km of river that would be inundated by the proposed Cedar Ridge Reservoir (D. McBride, pers. comm.), but it remains unclear of the species persists in this portion of the Brazos River.

My estimated value for survivorship is low (though likely a conservative underestimate because of limited recaptures of individuals) when compared to that of its sister taxa (25% for neonates and 50% for adults; Whiting 1993) and its congeners (e.g., 68% for *Nerodia taxispilota*; Mills 2002). Even though snakes are often considered to be poor model organisms for ecological studies that estimate survivorship (Turner 1977; Parker and Plummer 1987; Vitt 1987), several researchers have overcome sample size issues and successfully modeled snake survivorship with a higher level of precision for taxa such as elapids (Webb et al. 2002), viperids (Bruckerhoff et al. 2021), and colubrids (Whiting 1993; Mills 2002; Riedle 2014). In order to obtain a larger sample size and therefore a more accurate estimate of survivorship for *Nerodia harteri*, a study involving both longer duration and more frequent sampling trips during high activity periods is needed.

Detection of *Nerodia* spp. in this section of the Brazos River was most heavily influenced by search effort, wind velocity, ambient temperature, and humidity — variables that have been shown to influence detection of other snake species (e.g., *Ophiophagus hannah*; Rao et al. 2013). The naïve estimate of detection for *N. harteri* (0.33), higher than that of its sympatric congeners, is also well above detection probabilities reported for other herpetofauna (often <0.2; Durso et al. 2011; Steen et al.

2012; McGrath et al. 2015). Site-level covariates were not shown to influence site occupancy for *N. harteri*. This is likely because of the transect selection process used in this study. My transects were delineated based on *a priori* knowledge of *N. harteri* localities and assumed habitat preferences, as reported in previous studies (Scott et al. 1989; McBride 2009; S. Harding, unpublished data). This *a priori* knowledge is why, for example, other habitat variables such as rock presence were not analyzed.

Site occupancy for *N. erythrogaster* and *N. rhombifer* was predicted by the number of riffles per transect. Whereas these species are generally considered to be habitat generalists as adults (Keck 1998; Whiting et al. 1998; Laurent and Kingsbury 2003; Camper 2009), the young of both species have been observed using the same riffle habitat as *N. harteri* for a variety of reasons (pers. obs.; Scott et al. 1989; Rossi and Rossi 1999; McBride 2009). Subadult individuals of all three species have been observed sheltering under the same rock adjacent to a riffle (pers. obs.; Scott et al. 1989; McBride 2009). Unfortunately, the site-level nature of siteCovs in *unmarked* (i.e., a single value for the length of the transect) prevents further resolution and insights into the way(s) by which these sympatric watersnakes interact within the surveyed habitat.

Snakes actively prefer certain features within their environment (Weatherhead and Charland 1985; Burger and Zappalorti 1991; Weatherhead and Prior 1992) and this nonrandom use of habitat illustrates the importance of analyzing resource use on the microhabitat scale (Reinert 1993). Within surveyed portions of the Brazos River that do not contain established saltcedar shrubs (*Tamarix* spp.), riffle habitat was an important feature for all three species at the microhabitat scale. *Nerodia harteri* and *N. erythrogaster* selected for riffle microhabitat, but *N. rhombifer* tended to avoid riffles. Because of small sample sizes (few *N. erythrogaster* and *N. rhombifer* juveniles and/or neonates were found), the age classes of all 3 species were pooled together to model microhabitat selection. For this reason, it is not surprising that *N. rhombifer* selected against riffle microhabitat. *Nerodia rhombifer*, an exclusive piscivore, has been shown to forage in shallow water as a juvenile, but often forages in open, deeper water as an adult (Mushinsky et al. 1982; Manjarrez and Macías García 1991; Savitzky and Burghardt 2000). As such, *N. rhombifer* would not be expected to occupy the same riffle habitat that is selected by *N. harteri*.

Nerodia erythrogaster, considered the most terrestrial *Nerodia* sp. among the 3 species at my field sites (Keck 1998; Roe et al. 2004), has been noted to use a wide range of microhabitats (Hebrard and Mushinsky 1978). This species is piscivorous as a juvenile, but shifts to an anuran diet as an adult (Mushinsky et al. 1982). Anurans are often found along the shoreline, where *N. erythrogaster* has been documented foraging (Keck 1998), but anurans occurring along the Brazos River, particularly ranids (*Lithobates* spp.), can also be found sheltered under rocks within riffle habitat (pers. obs.). For this reason, riffle habitat might play a key role in foraging for both juvenile and adult *N. erythrogaster*. Patterns of riffle microhabitat selection in sites containing saltcedar were similar for *N. rhombifer* and *N. erythrogaster*. For *N. harteri*, however, selection for riffle habitat increased. The species was 35 times more likely to inhabit riffle microhabitat in sites containing saltcedar, as opposed to being only 8 times more likely to occur in those sites without saltcedar. The reasons for such a strong increase in selection for riffle habitat are not clear, but both results are not surprising, given the species is known to be a riffle specialist.

The presence of *Nerodia harteri* correlated positively with canopy cover in all surveyed transects, and I observed adult *N. harteri* basking on the limbs of trees along the riverbanks. Mushinsky and Miller (1993) found that predation pressure strongly influenced watersnake behavior. Higher levels of shoreline vegetation might help obscure *N. harteri* from avian predators (e.g., wading birds) found in this section of the Brazos River (cf. Lind 1990; Greene 1993; Mills 2002; Gardiner et al. 2015). *Nerodia erythrogaster* and *N. rhombifer* tended to occur in portions of the watershed with less canopy closure, consistent with the findings reported for these, and other snake species (Hebrard and Mushinsky 1978; Pike et al. 2011; Maddalena et al. 2020). The reasons for this difference in preference for the amount of canopy closure among the 3 species of *Nerodia* are unclear. By virtue of having larger body sizes than *N. harteri*, *N. erythrogaster* and *N. rhombifer* might not experience the same overall predation pressure from terrestrial and aquatic predators (Stamps 1983; Mushinsky and Miller 1993; Lind and Welsh 1994).

The preferences among these sympatric watersnakes for habitats having different levels of canopy cover might be explained by differences in body size and their physiological consequences. *Nerodia erythrogaster*, as the most terrestrial representative of this community, would seem to have a greater tolerance for desiccation (Keck 1998; Gibbons and Dorcas 2004; Roe et al. 2004), and therefore might seek microhabitat characterized by open canopy structure for more effective thermoregulation. Smaller snakes, such as *Nerodia harteri*, have a higher surface area to volume ratio and therefore experience changes in body temperature more quickly than that of larger-bodied snakes– such as *N. erythrogaster* and *N. rhombifer* (cf. Pough and McFarland 1976; Sanders and Jacob 1981; Bittner et al. 2002). Thus, *N. harteri* would need to seek refuge from direct sunlight more quickly than its congeners and select shaded microhabitat that decreases its rate of evaporative water loss (Scott et al. 1989; Winne et al. 2001; Gibbons and Dorcas 2004; Eskew et al. 2009).

Williams (1969) reported observing *Nerodia paucimaculata* basking on saltcedar branches (*Tamarix* spp.). Connections between *N. harteri* population declines and saltcedar establishment have been suggested (e.g., Scott et al. 1989; McBride 2009; Rodriguez et al. 2012), but patterns of *Nerodia* spp. habitat selection in relation to saltcedar are unresolved. In the surveyed reaches of the Brazos River watershed, I found that *N. rhombifer* was slightly more likely to occur in stretches of river having increased saltcedar density along the banks, while *N. erythrogaster* was slightly less likely to be found in those areas. Considering *N. erythrogaster* already tended to avoid greater levels of canopy closure, it is not surprising that this species was selecting against shoreline with established *Tamarix*. It is also not surprising that *N. rhombifer*, a riverine habitat generalist (Kofron 1978; Mushinsky et al. 1980; Laurent and Kingsbury 2003), would tend to associate with saltcedar habitat. Other species of habitat generalists not only are tolerant of habitat alteration that follows saltcedar establishment, but are also among the most successful species in areas dominated by *Tamarix* spp. (Segura et al. 2007; Bateman et al. 2013). Similarly, it is not surprising that saltcedar would be avoided by *N. harteri*, a habitat specialist.

Although saltcedar was used as site-level covariate for occupancy modeling, the single-value nature of siteCovs led to contrasting interpretations about *Nerodia harteri* tolerance of saltcedar. Analyzing saltcedar at the level of the transect indicates that *N. harteri* is somewhat tolerant of saltcedar, up to densities of roughly 20%. Examining the influence of saltcedar at a smaller spatial scale, however, indicates that *N. harteri* is intolerant of the shrub at bank vegetation densities higher than 1.0%. When managing species of conservation concern, analyzing habitat use at multiple scales is necessary to detect where selection is actually occurring (Beasley et al. 2007). Robson and Blouin-Demers (2021) found that habitat selection in *Heterodon platirhinos* varied based on the spatial scale being analyzed. In the Brazos River watershed, analyzing habitat selection at the microhabitat level is necessary because of the potential for saltcedar to alter the foraging habitat of juvenile *N. harteri* (e.g., increased sedimentation that reduces riffle habitat; Hereford 1984; Pollen-Bankhead et al. 2009; Row and Blouin-Demers 2016). Such alteration could have negative consequences for a species already facing intense selection pressures (e.g., river impoundment, stochastic changes in climate, etc.; Scott et al. 1989; Gibbons and Dorcas 2004; McBride 2009; Vogrinc et al. 2018).

The sister taxa, *Nerodia harteri* and *N. paucimaculata*, evolved in a dynamic habitat that has historically experienced seasonal fluctuations in environmental conditions (Whiting et al. 2008). Increasingly, however, severe weather phenomena — such as the exceptional drought in the early 2010s (D4-level; NDMC), and the 2021 record-breaking winter storm, when sections of the Brazos River froze over completely (NOAA 2021) — could threaten these habitat specialists. Saltcedar, as a generalist and more disturbance-tolerant species than other riparian vegetation, is able to both tolerate and colonize during events such as fire, flood, and drought (Sher 2013). Upper reaches of the Brazos River have experienced channel narrowing associated with *Tamarix* (Brotherson and Field 1987), but the portion of the Brazos River that I surveyed has not yet reached the monoculture status of *Tamarix* in the western portion of the U.S. (pers. obs.; Hink and Ohmart 1984; Taylor et al. 1999; Webb et al. 2007). Minimizing saltcedar establishment and spread can promote herpetofaunal diversity (Bateman and Ostoja 2010), would seem not to impact *N. erythrogaster* and *N. rhombifer*, and would likely benefit *N. harteri*.

The patterns of transect-level and microhabitat-level selection indicate that *Nerodia harteri*, *N. erythrogaster*, and *N. rhombifer* are partitioning their resources to some degree. Whereas Toft (1985) suggested that diet is the resource partitioned first among members of a snake community, evidence of partitioning either diet (Mushinsky et al. 1982; Luiselli 2006a; Halstead et al. 2008; Durso et al. 2013; Perkins 2016) or habitat (Reinert 1984; Keck 1998; Laurent and Kingsbury 2003; Luiselli 2006b; Steen et al. 2014) within snake communities has been documented. The sympatric watersnakes occurring in the Brazos River watershed appear to segregate by foraging habitat (sensu Roe et al. 2004; Eskew et al. 2009; Butterfield et al. 2020), which likely reflects the distribution of their prey within the community (Vitt 1987; Arnold 1993; Reinert 1993).

Whereas the watersnakes encountered in the surveyed transects all forage in shallow riffles as juveniles (cf. Hailey and Davies 1986; Mills 2002), the foraging habits of the adult life-history stages might lead to resource partitioning (Lind 1990; Savitzky and Burghardt 2000). *Nerodia erythrogaster*, piscivorus as a juvenile, eats frogs as an adult (Mushinsky and Lotz 1980). Morphological changes linked to ontogeny in *N. erythrogaster* facilitate its adopting a foraging method that is distinct from that of its piscivorus congeners (Mushinsky et al. 1982; Vincent et al. 2007; Perkins 2016). The foraging behavior of adult *N. rhombifer* described by Mushinsky et al. (1982), is likely beneficial for catching larger fish in deeper water (Manjarrez and Macías García 1991; Savitzky and Burghardt 2000; Perkins 2016). Much of the knowledge on the foraging method of adult *N. harteri* is inferred from *N. paucimaculata*, which is known to slowly swim along the bottom of a riffle, where it searches for larger fish under rocks (Greene 1993). I documented a similar behavior in an adult *N. harteri*, where an individual was slowly cruising the bottom of a relatively deeper riffle (~0.5 m), pushing its head around the rocks scattered at the bottom (pers. obs.). My observations support the idea that *N. harteri* also experiences an ontogenetic shift, not of prey type (all gut content recovered from the species appeared to be small cyprinids [e.g., red shiners; *Cyprinella lutrensis*]), but of foraging method and location within riffle habitat. Juvenile *N. harteri*, much like

N. paucimaculata, are known to anchor their tail to substrate in shallow riffles, where they remain motionless until striking at a passing minnow (Rose 1989; Greene 1993; K. Fleener, pers. comm.). Taken together with the analyses of macro- and microhabitat selection, my observations of foraging activities also support the interpretation that *N. harteri*, *N. erythrogaster*, and *N. rhombifer* are partitioning their use of habitat within the Brazos River watershed.

Conclusion

The future of *Nerodia harteri* throughout its range remains uncertain. There are breeding populations on the Clear Fork of the Brazos River and neonate individuals can be reliably found in suitable riffle habitat in Autumn. However, sections of river where this snake species had been reported by Scott et al. (1989) and McBride (2009) now appear to be unoccupied. The causes of the contraction in the distribution of this endemic snake are unclear, but the invasive saltcedar shrub (*Tamarix* spp.) might play a role. *Nerodia harteri* appears to select habitat characterized by riffle presence and increased levels of shoreline vegetation, but avoids those sections of the watershed where saltcedar has established. Competition between *N. harteri* and its sympatric congeners, *N. erythrogaster* and *N. rhombifer*, does not appear to be a constraint because these species partition their habitat, likely as a result of the different distributions of prey species (Gelwick 1990; Greenberg 1991; Sepulveda and Layhee 2015; Cloyed and Eason 2017; Cruz-Sáenz et al. 2019). Continued, frequent monitoring of the species is needed to gain a better understanding of why *Nerodia harteri* continues to experience a population decline, and how much of a given population survives from one year to the next. Habitat management, such as preservation of riffle habitat — crucial for juvenile foraging success — and removal of saltcedar, might be necessary for the persistence of the species.

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APPENDIX

Table A-1: Snake species encountered during surveys along the Brazos River, Texas, from May 2020 to October 2021, including the number of individuals observed and frequency of occurrence.

Clade/Species	Total number of individuals observed	Proportion of total observations
Leptotyphlopidae		
Rena dulcis	1	0.5
Viperidae: Crotalinae		
Agkistrodon piscivorus	2	1.1
Colubridae: Colubrinae		
Pantherophis obsoletus	1	0.5
Pituophis catenifer	1	0.5
Colubridae: Natricinae		
Haldea striatula	1	0.5
Nerodia erythrogaster	26	13.8
Nerodia harteri	42	22.3
Nerodia rhombifer	55	29.3
Storeria dekayi	2	1.1
Thamnophis proximus	52	27.7
Unidentified *Nerodia* sp.	5	2.7
Total	188	100

VITA

After her secondary education at Reicher Catholic High School, Waco, Texas, in 2014, Jessica Yates attended Texas Christian University in Fort Worth, Texas, where she researched the diet of phrynosomatid lizards, and completed a Bachelor's of Arts in Biology in 2018. She spent her free time at Cameron Park Zoo, in Waco, where she worked with a variety of taxa and furthered her love for animals and public outreach. In January 2020, she entered the Graduate School at Stephen F. Austin State University, and received a Master of Science in Biology May of 2022.

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