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Detection, Occupancy, Abundance, and Mercury Accumulation of the Alligator Snapping Turtle (Macrochelys temminckii) in Texas

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DETECTION, OCCUPANCY, ABUNDANCE, AND MERCURY ACCUMULATION OF THE ALLIGATOR SNAPPING TURTLE (*MACROCHELYS TEMMINCKII*) IN TEXAS

By

David Rosenbaum, Bachelor of Science

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Stephen F. Austin State University
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DETECTION, OCCUPANCY, ABUNDANCE, AND MERCURY ACCUMULATION OF THE ALLIGATOR SNAPPING TURTLE (*MACROCHELYS TEMMINCKII*) IN TEXAS

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ABSTRACT

Land use practices and physical alterations of ecosystems result in habitat loss and fragmentation, while chemical alterations, such as pollutant input, reduce habitat quality and health of exposed organisms. Here, I investigated the effects of watershed- and local-scale environmental variables on the occupancy, abundance, and mercury accumulation of a threatened aquatic species (*Macrochelys temminckii,* i.e., alligator snapping turtle) within the southwestern periphery of its distribution. Hierarchical modeling suggested the distribution of the species is more affected by watershed-scale land-cover than local habitat, and provided a baseline estimate of average species abundance across its range in eastern Texas. Abundance and occupancy were predicted by geographic location, and occupancy associated positively with forest cover. Mercury concentrations were predicted by environmental features at multiple scales, whereas body size had little effect. This research corroborates evidence that land use impacts aquatic species, as well as the susceptibility of aquatic systems to mercury accumulation.

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Detection, Occupancy, and Abundance of the Alligator Snapping Turtle (*Macrochelys temminckii*) in Texas

INTRODUCTION

Freshwater ecosystems are experiencing habitat alteration and species declines worldwide (Wohl 2019). Direct anthropogenic modifications such as impoundments commonly result in flooding, temperature shifts, flow rate changes, microhabitat homogenization, and siltation (Benke 1990, Magilligan and Nislow 2005, Riedle et al. 2005, Wohl 2019). Land-use practices (e.g., agriculture, deforestation) along riverine systems reduce riparian habitat and alter aquatic habitat by increasing temperatures, runoff, and photic input, and decreasing submerged microhabitat structure (e.g., logs and overhanging trees) utilized by myriad organisms (Rozas and Odum 1988, Pocewicz and Garcia 2016). These modifications lower habitat suitability for many aquatic species, and can have cascading effects on the structure and function of these ecosystems (Scott 2006).

Understanding spatial and temporal trends in the occurrence and abundance of organisms is integral to biodiversity monitoring (Kéry and Schmidt 2008, Lindenmayer et al. 2012, Prowse et al. 2021). Occurrence is used to determine species richness in spatially defined communities, and knowledge of species distributions in space and time can influence regional management practices (Gaines et al. 1999, Parish et al. 2021). Similarly, abundance indices are often used for species-level monitoring efforts to infer population dynamics, and importance of areas for conservation. Comprehension of processes that determine trends among species and communities are also important to inform conservation strategies (Myers and Gibbs 2013).

Several general macroecological patterns in abundance across geographic ranges of organisms have been observed. Among these is a decrease in abundance from core portions of ranges to peripheral locations (Lawton 1993, Doherty et al. 2003). However, in monitoring efforts, this apparent pattern in abundance is confounded by detection probability (*p*), as the two parameters are intrinsically linked (Tanadini and Schmidt 2011). When the abundance of a species is high, *p* will also be high, as the chance of encountering any one individual will be higher (i.e., density-dependent detection; Doherty et al. 2003, Lawton 1993, Royle and Nichols 2003). Detectability may also be dependent on other factors, including environmental characteristics (e.g., Price et al. 2011, Durso et al. 2011). When estimating distributional extent and abundance, it is important to account for imperfect detection (i.e., $p < 1$) and its potential variation across space to avoid underestimates (Mackenzie et al. 2006).

Freshwater ecosystems constitute only 0.8% of the earth's surface, yet they provide habitat to roughly 80% of turtle species (Dudgeon et al. 2007, Mitchell and Buhlmann 2009). Turtle populations are susceptible to declines from habitat degradation (Lovich et al. 2018) and direct exploitation (Congdon et al. 1994, Heppell 1998, Howey and Dinkelacker 2013). Turtles typically exhibit slow growth rates, delayed sexual maturity, low clutch and hatchling survivorship, large temporal intervals between reproduction, high adult survivorship, and long lifespans (Congdon et al. 1994, Heppell 1998, Howey and Dinkelacker 2013, Webb et al. 2002). Long generation times may correspond with a slower evolutionary rate (Martin and Palumbi 1993), which could leave turtles less likely to adapt and persist in response to increased rates of environmental change. Furthermore, these traits cause reliance on high adult survivorship for population persistence, which increases susceptibility to overexploitation and extirpation (Reed et al. 2002).

Persistence of aquatic turtle species is integral to the function of riverine systems and communities. Eggs and small individuals are preyed upon by a variety of animals, making them vital trophic links between aquatic and terrestrial systems (Ernst et al. 1994). Many species are important or even keystone consumers themselves (Lovich et al. 2018). For example, herbivorous and omnivorous turtle species affect plant communities both as agents of seed dispersal and by increasing germination rates by passing fruit through their digestive tracts (Moll and Jansen 1995, Blake et al. 2012). Furthermore, turtles are important reservoirs of matter (e.g., phosphorus) in ecosystems, as some species are capable of constituting a large percentage of biomass (Iverson 1982, Congdon et al. 1986, Sterrett et al. 2015).

Environmental and anthropogenic impacts on aquatic turtles are often inferred from hoop trap surveys (e.g., Mota et al. 2021, Ostovar et al. 2021, Hollender and Ligon 2021). Using this monitoring method, counts of turtles across survey sites and through time are standardized to a measure of catch per unit effort (CPUE) using trapping effort, which is the product of the number of traps deployed and the number of nights they are set (trap-nights). CPUE is often interpreted as an index of relative abundance, which requires the assumption that p is only influenced by abundance (N). Under circumstances that p is heterogeneous across sites for reasons other than variation in N, CPUE among sites will be differentially biased and not indicative of a constant proportion from each sampling unit (White and Bennetts 1996), rendering its interpretation as relative abundance imprecise. Hoop trap surveys often take place at large spatial scales (Wagner 1994, Rudolph et al. 2002), over a variety of environmental conditions and habitat types (Riedle et al. 2005), and across long periods of time (Trauth et al. 2016). This leaves potential for environmental heterogeneity between survey conditions, which can influence p of turtles (Morreale et al. 1984). There are always uncontrollable factors in field settings, which may limit the use of CPUE as an informative index (Mackenzie et al. 2006).

Furthermore, because hoop trapping is a passive capture method, detection is reliant on the behavior of turtles, as opposed to extrinsic variables (e.g., observer experience) that influence p in other wildlife monitoring contexts. Understanding detectability in the context of hoop trap surveys has utility beyond that of a nuisance parameter. It may also provide valuable insight into turtle ecology. As a result, some aquatic turtle studies have accounted for and modeled p (Stokeld et al. 2014, Johnson 2020, Dreslik et al. 2017, Sterrett et al. 2010, Buchanan et al. 2019), and this procedure is common practice with contemporary wildlife monitoring efforts (Kéry and Royle 2016).

Hoop trap surveys have contributed much of the current ecological understanding of patterns in distribution and abundance of the aquatic turtle *Macrochelys temminckii* (alligator snapping turtle) (e.g., Boundy and Kennedy 2006, Huntzinger et al. 2019, Jensen and Birkhead 2003, Riedle et al. 2005, Shipman et al. 1995, Howey and Dinkelacker 2013). Many studies using these surveys assume CPUE to be an adequate proxy of relative abundance (Folt and Godwin 2013, Huntzinger et al. 2019, King et al. 2016, Lescher et al. 2013). However, with a few exceptions (Johnson 2020, Dreslik et al. 2017), hoop trap surveys do not explicitly account for environmentally-caused variation in *p*. Nevertheless, CPUE is the only index available for inference on the relative abundance and distribution of *M. temminckii* across its range. Wild populations of *M. temminckii* are difficult to monitor due to their cryptic nature in difficult-to-access habitat, their occurrence over a wide range, and long generation times.

Habitat alteration and harvest are primary threats to the persistence of *M. temminckii* (Riedle et al. 2005). Consequently, states where it occurs have implemented protective regulations or, at minimum, recreational harvest limits (Louisiana Fisheries 2004, Reed et al. 2002). The U.S. Fish and Wildlife Service (USFWS) has considered listing *M. temminckii* under the Endangered Species Act since 1982 (Environmental Conservation Online System 2021), and in 2021 proposed Threatened status after completing a Species Status Assessment (SSA).

Prior surveys and historic distribution records indicate that the distribution of *M. temminckii* is contracting from its northern and western edges (e.g., Kentucky, Illinois, Oklahoma; Baxley et al. 2014, Bluett et al. 2011, Riedle et al. 2008a). Because of this, populations in Texas are important to examine in detail, as they represent the southwestern edge of the species' range. Relative to other states, data on the species in Texas are limited, but several sources (Hibbitts and Hibbitts 2016, Dixon 2013, Pritchard 2006) provide information on its occurrence in the state based primarily on presence-only data. In Texas, *M. temminckii* is known to occur within watersheds that drain into the Gulf of Mexico from the San Jacinto and Trinity Rivers eastward, as well as tributaries of the Mississippi watershed (Dixon et al. 2013, Hibbitts and Hibbitts 2016, Munscher et al. 2021). Major rivers encompassing the Mississippi watershed in this region are the Red, Sulphur, and Cypress Rivers (the latter two join the Red River in Louisiana), while the major Gulf-draining mainstems are the Sabine, Neches, Trinity, and San Jacinto Rivers.

Within watersheds where *M. temminckii* occurs, it may be found within permanent lacustrine and lotic waters, including river mainstems and smaller tributaries, swamps, sloughs, oxbows, and reservoirs (Sloan and Taylor 1987, Howey and Dinkelacker 2009). However, it exhibits specific microhabitat preferences (Harrel et al. 1996a, Riedle et al. 2006, Howey and Dinkelacker 2009, Riedle et al. 2015). Individuals are vagile, but maintain principal sites characterized by high overhead canopy cover and structure including bank undercuts, beaver dams, submerged trees and overhanging vegetation (Riedle et al. 2006, Howey and Dinkelacker 2009, Moore et al. 2014). The seemingly obligate relationship of the species with areas that have submerged structure and cover may be due to higher food abundance in these locations (e.g., fishes, fruit, and arthropods; Sloan and Taylor 1987, Howey and Dinkelacker 2009). Additionally, these microhabitats provide benefit to the species' ambush hunting strategy and ability to evade aquatic predators (e.g., river otters and American alligators; Ligon and Reasor 2007, Ernst et al. 1994, Howey and Dinkelacker 2009, Moore et al. 2014).

I conducted hoop trap surveys across the purported range of *M. temminckii* in Texas to gain insight on landscape and local habitat variables that influence and predict its distribution and patterns of abundance. Detection and count data obtained by field sampling enabled analysis of both occupancy and abundance of *M. temminckii*, as well as the environmental variables that influence *p*. Modeling occupancy is a robust method of inferring distribution, as it requires nondetection data in addition to presence data, unlike most species distribution models (Kéry and Royle 2016). By modeling occupancy and abundance together, the degree to which detection/nondetection data are sufficient to approximate abundance can be ascertained (Linden et al. 2017), as can the extent to which local density of turtles may influence detection probability (Tanadini and Schmidt 2011).

Because studies on *M. temminckii* suggest lower capture rates and activity in temperature extremes brought about during summer and winter months (Munscher et al. 2020, Riedle et al. 2006, Fitzgerald and Nelson 2011), I predicted a decrease in *p* during summer months and during warmer water temperatures. Because the morphology of *M. temminckii* is conducive to greater hydrodynamic drag relative to other turtles, and well adapted to benthic habits, I posited that increased flow velocity would decrease *p*. I also tested the effect of lunar phase on detection after noticing zero captures from 4 site visits conducted during and near the full moon, which was an anecdote of low *M. temminckii* capture rate on bright nights (Pritchard 2006). In regard to trapping efficacy, I predicted that density of traps would positively influence *p*. In regard to occurrence, I hypothesized a positive association with channel sinuosity, as more sinuous waters should have more low-energy pools that accumulate vegetation and woody debris that the species associates with, and that increased signs of human presence would negatively associate with occupancy. On a watershed scale, I hypothesized that increased proportions of wetland cover and forest − indicators of *M. temminckii* habitat availability − would increase occupancy probability and abundance, while greater developed and agricultural watershed cover would show the opposite relationship by reducing habitat suitability.

METHODS

Study Area

In April to October 2020 and March to August 2021, I conducted surveys in various water bodies representing habitats in which *M. temminckii* is known to occur: reservoirs, oxbows, sloughs, river mainstems, and tributaries. In a previous survey of the species' distribution in Texas, 21 sites throughout watersheds of its known range and two additional sites beyond its known range within the Brazos watershed were surveyed (Rudolph et al. 2002, Rosenbaum et al. in press). I resurveyed 22 of these 23 sites, as well as an additional 29 sites in counties that *M. temminckii* is suspected or known to inhabit, but either lack records, or have contradictory reports regarding its occurrence (Dixon 2013, Munscher et al. 2020, Rosenbaum et al. in press), for a total of 51 sites.

Site Selection

In the previous study, sites were purposively selected to represent every river drainage the species is known (i.e., Red, Sulphur, Cypress, Sabine, Neches, Trinity, San Jacinto) or suspected (i.e., Brazos) to occur (Appendix 1; Chris Collins, pers. comm., April 2020). This precluded a probabilistic site selection procedure. Additional survey sites were limited to a specific set of counties to help fill knowledge gaps of the Texas distribution of *M. temminckii*: Camp, Cass, Chambers, Cherokee, Delta, Ellis, Fort Bend, Grayson, Hunt, Kaufman, Lamar, Navarro, Rockwall, Trinity, Upshur, Van Zandt, and Waller counties (Rosenbaum et al. in press). I used three criteria to determine if aquatic habitats in these locations were suitable for trapping: 1) accessibility via public access points or landowner permission (*sensu* Sweeten and Ford 2016), 2) navigability by foot or boat, and 3) no habitat constraints (i.e., limited channel depth and width) that would prevent submergence of trap funnels. In both studies, only sites that were permanent and exhibited at least ephemeral connection with tributaries were sampled due to the predominantly aquatic habits and poor overland dispersal ability of *M. temminckii*.

Because of the criteria used in sample selection, there are important implications to consider when making statistical population inferences from analyses. Estimates and predictions from models developed from these samples are only applicable to large, permanent water bodies that exhibit at least indirect connectivity with river mainstems of eastern Texas. Sampling such areas will positively bias estimates above those that would be expected from probabilistically sampled sites. Furthermore, these sites have the potential to become reference monitoring sites for the species.

Field Surveys

I used single-funnel, finger-throated, four-hoop traps (hoop diameter = 1.2 m; mesh size = 2.54 cm) baited with fish to detect *M. temminckii*. I predominantly used cuts of *Cyprinus carpio* as bait, but *Ictiobus* spp., *Morone* spp., *Aplodinotus grunniens,* and *Ictalurus* spp. were occasionally used to supplement *C. carpio*. I suspended fish from the rear hoop of each trap in a holding canister. Each canister was constructed of 7.6 cm x

30.5 cm PVC pipe with 36 1.3 cm-diameter holes to aid in dispersal of bait scent. This method prevented bait consumption and ensured continued scent dispersal after one or more turtles entered a trap.

Site visits were standardized to 3 consecutive surveys per site, with 15 baited hoop traps deployed per survey. Therefore, I allocated 45 trap-nights of survey effort to most sites. However, during 8 site visits, logistical constraints such as flood events and trap theft resulted in fewer surveys and fewer hoop traps per survey (Appendix 2). Two sites were allocated only two surveys each, and one site was only allocated one survey.

Each of the 3 surveys at a site began when traps were baited and deployed. In lotic waters, I deployed traps upstream of aquatic structures, undercuts, or low energy pools, when available. In lentic systems, I secured traps near banks with openings facing deeper water and aquatic structure, or tied them to trees and woody debris in open water. On average, across all surveyed sites, the mean linear distance of each trap to its nearest neighbor was 105m. I would conclude each survey after traps were left in place overnight (approximately 24hr) and then checked for captures. All *M. temminckii* caught were measured, sexed, and marked before their release. I then replaced bait prior to re-deploying traps, at which point a subsequent survey began. Fresh bait was used for each survey because *M. temminckii* CPUE is documented to increase with the use of fresh fish (Jensen 1998). This also assured no reduction in bait effectiveness between surveys, thereby maintaining independence between consecutive surveys. Conducting surveys consecutively minimized temporal environmental heterogeneity (e.g., water temperature, flow velocity) that may bias *p*, and provided the best possible assurance that each site was closed to changes in occupancy status and abundance during surveys. I determined per-site CPUE as the number of individual *M. temminckii* captured divided by the total number of trap-nights across all surveys. Recapture events were not included in the calculation (*sensu* Boundy and Kennedy 2006, Lescher et al. 2013).

Habitat variables

I recorded the presence or absence of floating vegetation, submerged and emergent vegetation, and woody debris within a 5-meter radius of each trap. Additionally, I measured canopy cover above each trap opening with a spherical densiometer (*sensu* Strickler 1959). At the opening of each trap, 4 densiometer readings were taken: one oriented in the direction the trap opening faces (downstream in lotic waters), one oriented toward the rear of the trap (i.e., upstream), and one to each side perpendicular to the opening. This enabled a 360° estimate of canopy cover above the entrance of each trap (Strickler 1959). I recorded maximum water depth at trap opening, wetted channel width, and decimal degree coordinates (to 6 decimal places; WGS 84 datum) at each trap. Habitat variables collected at each trap were included in site-scale analyses of occupancy and abundance by averaging measures within each site (*sensu* Perinchery et al. 2011). In this context, each trap can be considered as a sampling point, the composite of which represent the site.

Many sitewide variables were related to anthropogenic influence and human accessibility. These included the number of passive fish lines (i.e., trotlines, limblines, juglines; hereinafter collectively referred to as trotlines) observed, as well as binary categorical variables (Table 1.1). These were compiled into an additive index to serve as a covariate of occupancy and abundance that approximated human accessibility (hereinafter referred to as human accessibility index). Trotline number was the only variable used in the index that was not categorized by presence or absence. Trotlines are often abandoned by fishermen to remain *in situ*, and do not degrade quickly. Because of this, their numbers accumulate in frequently fished areas, and can give insight on long-term fishing pressure. However, not all trotlines are detected in sites because of observation error, so numbers are likely underestimated. To account for uncertainty in counts, the total numbers observed were assigned to 1 of 3 ordinal categories, each of which corresponded with an additive value for the index (Table 1.1). Other site variables collected on site included surface water temperature (°C) and flow velocity (m/s). The latitude and longitude (decimal degree coordinates; WGS 84 datum) of site access points were collected and used as site covariates of occupancy and abundance after I documented a strong unimodal latitudinal gradient in CPUE across the watersheds surveyed (Rosenbaum et al. in press).

Table 1.1. Factors used to quantify human accessibility index values of each site.

Factor	**Points to index**
Presence of footpath(s) to (but not along) waterbody	1
Presence of footpath(s) also running along waterbody	1
Presence of fishing dock(s)	1
Presence of other structure(s) (e.g., duckblinds)	1
Presence of major highway	4
Presence of county road or farm to market road	3
Presence of small paved road (e.g., dead end road or park road)	2
Presence of unpaved road	1
Does site have restricted property access?	-1 if yes
Is site within or adjacent to non-primitive campsite or park?	1 if yes
Presence of boat lanes or channelized flow	1
Presence of full access boat ramp	2
Presence of restricted boat ramp (e.g., no motors allowed, private property)	1
Presence of evident jon boat use	1
Presence of fishing lines in trees	1
Presence of traps	1
Number of trotlines:	
1 - 5	2
6 – 15	3
> 15	4

I calculated the average nearest neighbor linear distance (NND) of traps per site using ArcGIS Desktop 10.7.1 (ESRI, Redlands, CA, USA) to quantify trap spacing. I considered ordinal date as a survey-level covariate to capture potential seasonal variability in p. Dates of each survey were calculated using statistical software R 4.0.5 (R Core Team 2021) with the package *lubridate* (Grolemund and Wickam 2011). I obtained lunar phase of each survey in radians using the R package *lunar* (Lazaridus 2015).

I acquired landscape-scale covariates with ArcGIS Desktop 10.7.1. All georeferenced data used with the software were projected to Texas Statewide Mapping System of the North American Datum (NAD) of 1983. I obtained land cover type data from the conterminous United States National Land Cover Database updated in 2019 (NLCD 2019) (Dewitz and USGS 2021). From the 16 cover categories into which this dataset organizes land of the United States, I developed 4 broad cover categories for analysis: total forest cover (the aggregation of NLCD-defined deciduous, evergreen, and mixed forest cover), open field cover (the aggregation of NLCD-defined pasture/hay and crops), developed land cover (the aggregation of all NLCD-defined developed categories), and total wetland cover (the aggregation of NLCD-defined woody and emergent herbaceous wetlands). Differences between each of the NLCD cover types in the compiled categories are assumed to negligibly affect *M. temminckii*. For example, the species is known to occur in both woody wetlands and herbaceous wetlands dominated by plants such as *Cephalanthus* (buttonbush) or *Typha* (cattail) (Harrel et al. 1996a). Furthermore, compiling similar cover types into one reduces the number of parameters to model.

I delimited sites by subwatershed (12-digit Hydrologic Units) polygons provided by the Watershed Boundary Dataset of USGS (USGS 2020). These boundaries are delineated by topography and surface water flow, so define biologically relevant units of the landscape (USGS 2009). For cases in which more than one site occurred in the same subwatershed polygon, only the first site surveyed was considered for further analysis to prevent repeat values. This resulted in 48 samples out of the 51 sites surveyed. I then calculated the proportions of the 4 land cover types in each subwatershed. I used National Hydrography Dataset (NHD) Flowline polylines limited to the farthest upstream trap and farthest downstream trap of each site to calculate site waterbody lengths. (USGS 2020). These values were standardized to the linear distance between these traps to quantify sinuosity. NHD and ArcGIS were also used to calculate the surface area of water trapped at each site using trap coordinates. In lotic sites, surface area was calculated as the average wetted channel width multiplied by flowline polylines used in sinuosity calculation. In lentic sites, area was calculated as the minimum convex polygon connecting trap coordinates, excluding sections encompassing land. These values were used to estimate average *M. temminckii* density from the average abundance estimate.

Data Analysis

To infer the distribution of the species within the study region, as well as variations in abundance, survey data were analyzed using hierarchical models each consisting of two submodels. In these models, one submodel describes false-negative error rates in observation data (detections/nondetections or count data), and is conditional on a second submodel describing a latent, unobservable state variable (the state or ecological process submodel; Kéry and Royle 2016). Site occupancy status (z) and site population size (N) during surveys were the latent variables considered. In the context of ecological studies, the false-negative error rate describes p.

All continuous covariate values used to model occupancy probability and abundance (Table 1.2) were z-standardized (Taillie et al. 2015, Kéry and Royle 2016). Prior to fitting models, Pearson’s correlation coefficients (*r*) were calculated for each pair of covariates. For pairs of covariates with $r > 0.6$, only one of the pair was considered for modeling to minimize collinearity.

Table 1.2. Descriptions and labels of covariates used to model detection, occupancy and abundance of *Macrochelys temminckii* in eastern Texas.

Ecological process covariates	**Covariate Name**	**Description**
Covariates describing geographic location	watershed	River mainstem the site is associated with (Mississippi, Sabine, Neches, Trinity, San Jacinto, Brazos, San Bernard).
	latitude	Y-axis geographic coordinate in decimal degrees (WGS 84 datum) of each site.
	longitude	X-axis geographic coordinate in decimal degrees (WGS 84 datum) of each site.
Covariates describing characteristics of subwatersheds	open water	Proportion of NLCD 19 -defined open water cover within the USGS subwatershed containing the survey site.
	forest cover	Combined proportion of NLCD 19-defined deciduous forest, evergreen forest, and mixed forest cover within the USGS subwatershed containing the survey site.
	open cover	Combined proportion of NLCD 19-defined pasture/hay and cultivated crop (i.e., agricultural land) cover within the USGS subwatershed containing the survey site.
	developed cover	Combined proportion of NLCD 19-defined developed open space, developed low intensity, developed medium intensity, and developed high intensity land cover within the USGS subwatershed containing the survey site.
	wetland cover	Combined proportion of NLCD 19-defined woody wetlands and emergent herbaceous wetlands cover within the USGS subwatershed containing the survey site.
Covariates describing local habitat characteristics within a site	dams	Number of dams between the survey site and the watershed's mainstem.
	sinuosity	Ratio of a water body's actual length contained by the most upstream and downstream traps, to the linear distance between the same points. This value is 1 for lentic systems, where the actual distance between points may be navigated linearly.
	HAI	Human accessibility index based on observations from each site's surveys to approximate the degree of human visitation pressure a site receives (Table 1.1).
	veg	Proportion of traps within a site where submerged or emergent vegetation was observed.
	debris	Proportion of traps within a site where emergent and/or submerged woody debris was observed.
	canopy	Average canopy cover percentage above traps set at a site.
	depth	Average water depth of traps set at a site.
Detection covariates	temp	Surface water temperature (°C)
	flow	Surface flow velocity (m/s) in the main channel of a trapped area.
	(continued)	

lunar	State of the moon along the lunar cycle (in radians) during a survey.
date	Ordinal day of the year; between 1 and 366.
NND	Average nearest neighbor distance of traps locations.

Model Selection and Assessment.— I analyzed models using frequentist inference and maximum likelihood estimation of parameters. Relative model fit was inferred with an information-theoretic perspective using likelihood, Akaike's Information Criterion corrected for overparameterization (AIC_c), and Akaike weights (w_i) (Burnham and Anderson 2002). To determine which covariates best predicted occupancy and abundance, I adopted a sequential-by-sub-model selection strategy (Morin et al. 2020), in which I first developed *a priori* hypotheses including combinations of *p* covariates while considering state processes constant across all sites (i.e., at their intercepts). Using the best-fit *p* sub-model, I independently ranked three suites of models categorized by covariates pertaining to either 1) geographic location, 2) subwatershed land cover, or 3) local habitat characteristics (Table 1.2). After fitting global models representing each of these suites, the variance inflation factor (VIF) of each covariate in the global model was calculated. If VIF of a covariate was greater than 5, it was dropped from analysis to minimize multicollinearity. All models were fitted using the R package *unmarked* (Fiske and Chandler 2011). Model selection was computed with the package *AICcmodavg* (Mazerolle 2020).

Static site occupancy model.— The simplest model considered was the static (i.e., single season) site occupancy model outlined by Mackenzie et al. (2002), which uses binary detection/nondetection data to estimate p of the considered species, conditional on site i being occupied, to in turn estimate occupancy probability (Ψ). The latent state variable, occupancy status (z_i) is also binary. Covariates were incorporated with a logit link function (Grace-Martin 2015). The following assumptions pertinent to consider with my sampling methods are implicit in this occupancy model:

1) z_i of site i does not change for the duration of the study. This assumption is reasonably met by the sampling procedure because of the limited timeframe over which repeat surveys occurred, and the propensity for *M. temminckii* individuals to adopt home ranges they move from infrequently (Trauth et al. 2016).

2) There is no unmodeled heterogeneity in p among sites (Mackenzie et al. 2006). Violating this assumption can negatively bias estimates of occupancy (Mackenzie et al. 2006), yet is inevitable in the context of most ecological studies across areas where abundance varies (Dorazio 2007, Royle and Nichols 2003, Tanadini and Schmidt 2011). This highlights an important consideration when using this model (See Royle-Nichols *N*-mixture model below).

3) Repeat surveys and sites are independent. Rebaiting traps between surveys minimized the risk of second and third survey outcomes depending on prior survey(s). However, *M. temminckii* that were caught in a trap on one survey were unlikely to be recaptured during subsequent surveys, which indicates there was a behavioral response

negatively influencing p in secondary and tertiary surveys. Despite this, there was no consistent pattern of decreasing counts with additional surveys (Appendix 2). If dependence between surveys were occurring, it was not apparent in the counts of turtles of each survey. I initially accounted for inter-survey dependence with a binary dummy covariate of p which was assigned a value of 0 for primary surveys and 1 for subsequent surveys (*sensu* Mackenzie et al. 2006). However, this did not exhibit a strong negative relationship with detection data, so dependence was assumed negligible and this covariate was not considered. Each site was sufficiently spaced to prevent one site's occupancy status to directly influence another's (i.e., no exchange of *M. temminckii* individuals between sites), and other potential sources of spatial dependence in occupancy were assumed accounted for by covariates.

I assessed the absolute fit of the global model representing each of the three covariate groups with the χ^2 goodness of fit described by Mackenzie and Bailey (2004) (*unmarked* function *mb.gof.test*). This test estimates an overdispersion parameter ($\hat{c}$), which is the ratio of observed χ^2 value to the mean χ^2 obtained from bootstrapped data (i.e., expected χ^2) with 1,000 parametrically bootstrapped resamples. This test also computes the probability that expected χ^2 is greater than or equal to the observed χ^2 under the assumption that the model is an adequate fit of the data (Mackenzie and Bailey 2004). To infer how many surveys are required to attain 95% confidence *M. temminckii* is truly absent at a site, I used the formula developed by McArdle (1990) *sensu* Ward et al. (2017), in which j is the required survey number and p is detection probability:

$$j = \frac{\log (1 - 0.95)}{\log (1 - p)}$$

Royle Nichols N-mixture model.— As stated above, an assumption of the static occupancy model is that p is homogenous among sites, or that heterogeneity is accounted for with covariates. For most animals, spatial variation in the latent variable abundance (N) is a certainty, and a predominant source of heterogeneity in p (Royle and Nichols 2003, Tanadini and Schmidt 2011). I fitted detection/nondetection survey data to the model described by Royle and Nichols (2003), which accounts for variation in p resulting from variation in N. This allowed inference on whether p is density-dependent in hoop trap surveys, as well as estimation of expected abundance (λ) to compare with observed counts (*sensu* Linden et al. 2017). Because abundance was modeled as a Poisson distribution, its covariates were incorporated with a log link function (Meyer 2020). Assumptions of this model are similar to those of the static site occupancy model (Doré et al. 2011). I tested the goodness of fit with 1,000 bootstrapped resamples.

Multinomial N-mixture model.— More precise estimates of abundance are possible with counts of individuals whose identities are known. To take advantage of my dataset of individual detections, I utilized multinomial *N*-mixture models that accommodated counts of individuals under a removal sampling protocol (Zippin 1956, Dorazio et al. 2005, Kéry and Royle 2016). The behavior of *M. temminckii* accommodates a removal protocol; a previously captured individual is unlikely to be detected during subsequent surveys so is conceptually “removed” from the local population. During the infrequent events that individuals were recaptured, they were simply identified and not counted (Appendix 2). With a maximum of 3 surveys per site, each individual at a site had 4 potential detection histories: 1 - -, 01 -, 001, or 000. Because there were more than two detection outcomes, the observation process was multinomial (Kéry and Royle 2016). Using this model enabled comparison with the RN and occupancy models to determine whether coarser detection/nondetection data can reasonably capture variation in λ as determined from count data, and whether inferences based on estimates of Ψ can serve to approximate those based on λ when count surveys are not feasible (Linden et al. 2017).

Preliminarily, I modeled abundance to follow a Poisson distribution. The absolute fit of this model to the data was determined with a χ^2 goodness of fit formulated for *N*-mixture models (R function *Nmix.gof.test*; Mazerolle 2020). Bootstrapping 1,000 resamples confirmed large degrees of overdispersion with $\hat{c} > 2$, indicating that variance in data was not equal to the mean. Thus, I modeled abundance as a negative binomial distribution (Kéry et al. 2005b) incorporating a dispersion parameter using the *unmarked* function *gmultmix*. This relaxed the assumption of spatial independence required by a Poisson distribution (White and Bennetts 1996). I used the $\hat{\lambda}_i$ of the AIC$_c$ best-fit model to condition an estimate of *N* at each survey site using Bayes' theorem with the *unmarked* function *ranef* (Fiske and Chandler 2011). In the context of this study, $\hat{\lambda}_i$ is interpreted as the expected number of individuals available for potential capture within the survey period. I used the formula described above (McArdle 1990) to calculate the number of surveys required to attain 95% confidence all *M. temminckii* available for capture had been detected at a site (this, of course, does not consider the reality that over longer periods of survey time, the assumption of site closure is more likely to be violated).

Model comparison.— I used Pearson's correlation coefficients (r) to determine correlations between λ estimated by the Royle-Nichols (RN) and multinomial *N*-mixture models, as well between Ψ estimates of the site occupancy model and λ estimates of the *N*-mixture models. I also assessed differences in absolute counts given by the two *N*-mixture models with least-squares regression (*sensu* Linden et al. 2017).

RESULTS

In 2020 and 2021, I conducted 2,153 trap-nights at 51 sites in 42 counties. This effort resulted in 238 detections of 221 *M. temminckii* and confirmed 60.7% of sites (n = 31) occupied. The highest number of captured turtles in a survey was 11, while the highest number of captures at one site was 17 (maximum CPUE = 0.378; Appendix 4). Of the 48 sites analyzed, overall CPUE was 0.105 turtles per trap-night, with an average per-site CPUE of 0.094. Southwestern and northeastern watersheds exhibited the lowest average capture rates (Fig. 1.1). No global model indicated significant overdispersion (Appendix 3).

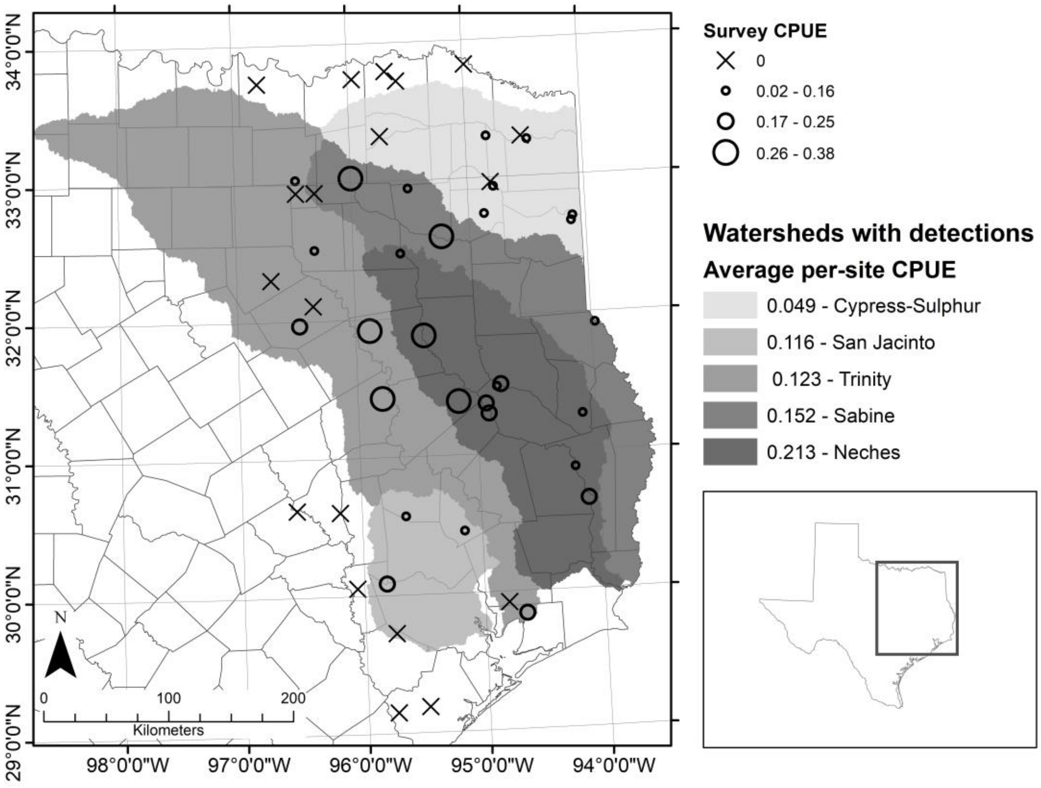

Figure 1.1. Site locations depicting variation in catch per unit effort (CPUE) of *Macrochelys temminckii* sampled from May 2020 to August 2021 in eastern Texas, United States. Note that CPUE averages of the Cypress and Sulphur watersheds are calculated separately from sites in the Red River mainstem watershed, where no individuals were detected.

Site occupancy model

Mean *p* (i.e., not considering site/survey heterogeneity) was estimated to be 0.77 (95% CI = [0.66, 0.85]). Under constant conditions, approximately two surveys (95% CI = [2,3]) would be required for 95% confidence of *M. temminckii* absence. Flow velocity, lunar phase, and trap NND distance indicated no strong pairwise correlations. As expected from temperate seasonality, temperature and ordinal date were moderately correlated (r = 0.59). Because VIF of all detection covariates was less than 3.6 in the global site detection submodel, all covariates were retained. Detectability of *M. temminckii* decreased with increased flow velocity (β_{flow}: -0.99, 95% CI = [-1.77, -0.21]). Lunar phase and trap NND also affected p, as the top model included them ($\beta_{lunar}{}^2$: 1.33, 95% CI = [0.54, 2.12]; β_{NND}: -1.80, 95% CI = [-3.01, -0.59]) (Table 1.3). After accounting for heterogeneity in p, mean $\widehat{\Psi}$ rose from just above the naïve estimate (0.62, 95% CI = [0.47, 0.75]) to 0.82 (95% CI = [0.58,0.93]).

Attempting to model the watershed of each site resulted in substantial variance inflation and standard errors for all models of occupancy and abundance. Therefore, only latitude and longitude were considered as geographic location covariates. $\widehat{\Psi}$ varied over a latitudinal gradient, but there was a relatively large degree of uncertainty with this relationship ($\beta_{latitude}{}^2$ = -3.63, 95% CI = [-8.54, 1.28]) despite the majority of nondetection sites being at extremes of latitude in the study area (Fig 1). $\widehat{\Psi}$ also declined towards the western edge of the study, but this was not strongly supported ($\beta_{longitude}$: 0.63, 95% CI = [-1.52, 2.78]; Table 1.3). Of the subwatershed hypotheses considered, forest cover alone was the best predictor of *M. temminckii* occupancy (β_{forest}: 2.89, 95% CI = [0.53, 5.25]) (Table 1.3, Fig. 1.2). Neither proportion wetland cover nor developed land cover were competitive predictors of occurrence on their own. However, agricultural land was negatively correlated with forest cover (r = -0.55), and consequently also exhibited a moderate negative relationship with Ψ (β_{open}: -0.92, 95% CI = [-1.88, 0.040]). All measured variables of in-stream habitat were poor predictors of occupancy (Table 1.3). Relationships between Ψ and all considered habitat variables were estimated to be positive, but standard errors were too large to warrant predictive use or inference.

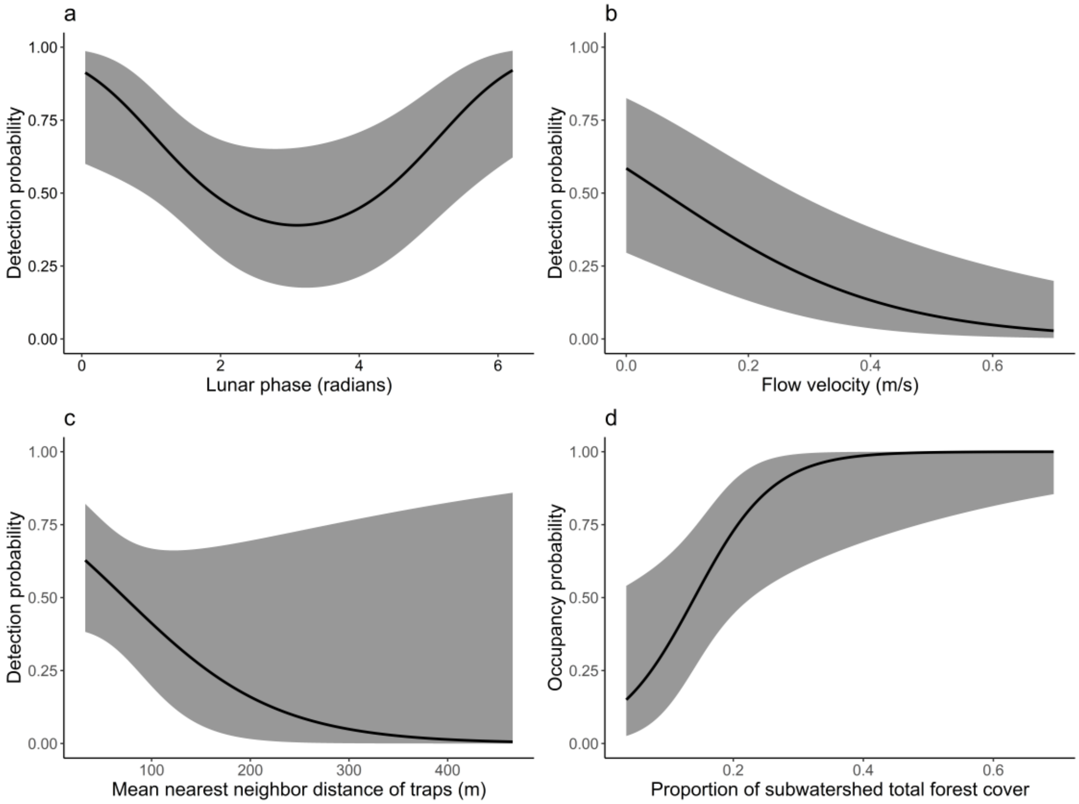

Figure 1.2. Predicted *Macrochelys temminckii* occupancy probability and detection probability from the top-ranked subwatershed occupancy model. (a) *M. temminckii* detectability is predicted to increase at new moons (0 and 6.28 radians), and decrease near the full moon (3.14 radians). (b) Increasing flow velocity and (c) trap nearest neighbor distance (NND) lower detection probability. Although NND was included in the lowest-AIC$_c$ detection model, its standard error inflated after adding covariates of occupancy. (d) High forest cover predicted high occupancy probability. Gray shading depicts 95% confidence intervals.

Table 1.3. Models of *Macrochelys temminckii* site occupancy with ΔAICc < 2. Models were fitted with data from (n = 48) locations within eastern Texas, United States. All models with covariates of occupancy utilize detection covariates from the lowest-AIC_c detection model. Refer to Table 1.2 for covariate definitions.

Model	***K***	**AIC_c**	**Δ AIC_c**	**w_i**	**LL**
Detection covariate models					
p(flow + lunar + lunar^2 + NND) Ψ(.)	6	143.28	0.00	0.59	-64.62
p(flow + lunar + lunar^2 + NND + date + temp) Ψ(.)	8	144.52	1.24	0.32	-62.42
Geographic location covariate models					
Ψ (latitude + latitude^2 + longitude)	9	129.78	0.00	0.99	-53.52
Subwatershed covariate models					
Ψ(forest)	7	132.88	0.00	0.54	-58.04
Local habitat covariate models					
Ψ(.)	6	143.28	0.00	0.49	-64.62
Ψ(canopy + debris)	8	144.36	1.08	0.28	-62.33

Royle-Nichols *N*-mixture model

The top RN *N*-mixture model retained the same covariates as the occupancy model (β_{flow}: -0.91, 95% CI = [-1.62, -0.21]; $\beta_{lunar}{}^2$: 1.27, 95% CI = [0.49, 2.06]; β_{NND}: -1.65, 95% CI = [-2.74, -0.57]). The importance of accounting for heterogeneity in *N* was revealed by the covariates granting greater w_i than that in the best occupancy model (Table 1.4), as well as lower relative $\hat{c}$ in global RN models with abundance covariates (Appendix 3). The mean probability of individual detection (i.e., without accounting for covariate influences) was 0.65 (95% CI = [0.48, 0.78]).

Detection/nondetection data underestimated counts of turtles. $\hat{\lambda}$ in the null RN model was 1.03 turtles (95% CI = [0.69, 1.55]), and due to the high estimated detection probability only rose to 1.18 turtles (95% CI = [0.74, 1.86]) after accounting for flow velocity, lunar phase, and trap NND. In contrast, the mean observed per-site count was 4.33 turtles. Even after accounting for *p*, abundance patterns were congruent with those shown by CPUE, in which counts varied unimodally over a latitudinal gradient (Fig. 1.1, Table 1.4). The relationship between latitude and abundance was stronger than with occurrence ($\beta_{\text{latitude}}^2$ = -0.83, 95% CI = [-1.36, -0.30]; Fig. 1.3). Analogous to occupancy, abundance was well-predicted by forest cover (for the top model, β_{forest}: 0.55, 95% CI = [0.18, 0.92]). However, with a relatively low w_i, the RN model indicated that forest cover did not have as great an influence on abundance as with occurrence. Local habitat variables were poor predictors of abundance, furthering the similarities in inferences produced by analyses of occupancy and abundance.

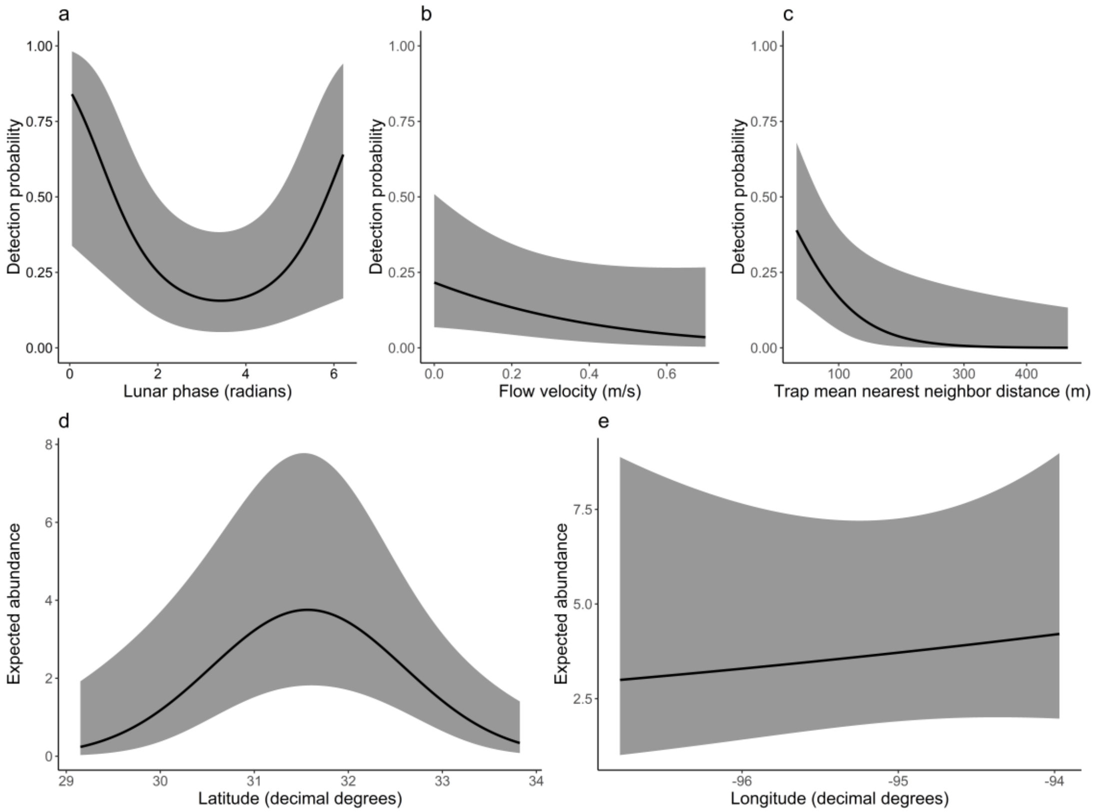

Figure 1.3. Predicted per-individual detection probability and predicted abundance based on the top-ranked Royle-Nichols *N*-mixture model. (a) Detection probability is highest during new moons (0 and 6.28 radians) and lowest near full moons (3.14 radians). (b) Flow velocity and (c) trap nearest neighbor distance were inversely correlated with detection. (d) Middle latitudes of the study area are modeled to have higher abundance. (e) Although lower longitudes in the study area granted lower predicted abundance, inference is limited due to large confidence intervals. Gray shading depicts 95% confidence intervals.

Table 1.4. Royle-Nichols *N*-mixture models of *Macrochelys temminckii* abundance and detection probability with ΔAICc < 2 (by convention, r is used to denote individual detection probability). Models were fitted using *M. temminckii* detection/nondetection data from ($n = 48$) locations in eastern Texas. All models with covariates of abundance utilize detection covariates from the lowest-AIC$_c$ detection model. Refer to Table 1.2 for covariate definitions.

Model	***K***	**AIC$_c$**	**Δ AIC$_c$**	**w_i**	**LL**
Detection covariate models					
r(flow + lunar + lunar^2+ NND) λ(.)	6	140.51	0.00	0.70	-63.23
r(flow + lunar + lunar^2 + NND + date + temp) λ(.)	8	142.91	2.39	0.21	-61.61
Geographic location covariate models					
λ(latitude + latitude^2 + longitude)	9	133.52	0.00	0.96	-55.39
Subwatershed covariate models					
λ(forest)	7	134.90	0.00	0.29	-59.05
λ(forest + wetland)	8	135.45	0.56	0.22	-57.88
λ(developed + forest)	8	136.44	1.55	0.13	-58.38
λ(crops + forest + wetland)	9	136.77	1.87	0.11	-57.01
Local habitat covariate models					
λ(.)	6	140.51	0.00	0.45	-63.23
λ(HAI)	7	142.34	1.83	0.18	-62.77

Multinomial *N*-mixture model

The mean probability of individual detection was estimated to be 0.38 (95% CI = [0.27, 0.49]) by the multinomial model— almost half that of the RN model estimate. Six surveys (95% CI = [4,9]) would be required for 95% confidence all *M. temminckii* available for capture are detected at a site. Water temperature was eliminated from multinomial detection submodels (VIF > 5). Flow velocity, lunar phase, and trap NND were important determinants of individual detection. However, the contribution of trap spacing to detectability was greater than indicated by the RN model, and while lunar phase was fitting as a predictor of species detection, it had less of an effect on numbers detected relative to other variables (Table 1.5). The top model included flow velocity (β_{flow}: -1.01, 95% CI = [-1.62, -0.41]) and trap NND (β_{NND}: -1.41, 95% CI = [-2.25, -0.57]) as covariates.

Mean $\hat{\lambda}$ estimated by the multinomial model was 5.46 (95% CI = [3.38, 8.81]) turtles before modeling heterogeneity in *p*, just above the average empirical per-site count. After accounting for heterogeneity in *p*, this estimate rose to 7.57 (95% CI = [4.57, 12.54]) turtles, revealing the effect of unfavorable trapping conditions and methods on CPUE. The multinomial model disclosed similar inferences of geographic location as the RN model ($\beta_{latitude}^2$ = -0.90, 95% CI = [-1.39, -0.42]; Table 1.5) despite the RN model overestimating detection and underestimating λ. However, forest cover was not a reliable predictor (β_{forest} = 0.25, 95% CI = [-0.20, 0.69]). Average density of *M. temminckii* was estimated to be 79 individuals/km^2, using $\hat{\lambda}$ = 7.57 and average per-site surface area of water trapped. The average length of channel surveyed was 0.931km, resulting in an estimated density of 8 individuals/channel km.

Using the top ranked multinomial *N*-mixture model (Table 1.5), $\widehat{N}_i$ of *M. temminckii* present during surveys ranged up to 28 individuals, 11 more than the maximum number observed at any site (Appendix 4). $\hat{\lambda}$ trended positively with CPUE. However, ranking sites in order of increasing *M. temminckii* using CPUE did not lead to the same result as $\hat{\lambda}$ (Appendix 4).

Table 1.5. Multinomial *N*-mixture models of *Macrochelys temminckii* abundance and detection probability with ΔAICc < 2. Models were fitted using *M. temminckii* count data from ($n = 48$) locations in eastern Texas. All models with covariates of abundance utilize detection covariates from the lowest-$\mathrm{AIC_c}$ detection model. Refer to Table 1.2 for covariate definitions.

Model	***K***	**$\mathrm{AIC_c}$**	**$\Delta\ \mathrm{AIC_c}$**	**w_i**	**LL**
Detection covariate models					
p(flow + NND)	5	51.90	0.00	0.69	-20.23
p(flow + lunar + lunar^2 + NND)	7	53.96	2.06	0.24	-18.58
Geographic location covariate models					
λ(latitude + latitude^2 + longitude)	8	47.14	0.00	0.91	-13.73
Subwatershed covariate models					
λ(.)	5	51.90	0.00	0.33	-20.23
λ(forest)	6	53.31	1.41	0.16	-19.63
Local habitat covariate models					
λ(.)	5	51.90	0.00	0.54	-20.23

Model Comparison

The three model types ranked the relative importance of variables– as well as the direction of their effects on occupancy and abundance– similarly, with the exception of habitat covariates with high standard errors. However, abundance was not predicted as well as occurrence by land cover covariates when count data were utilized. The top ranked RN and multinomial *N*-mixture models showed a strong relationship between $\hat{\lambda}_i$ values ($r = 0.98$), but species detection data significantly underestimated λ_i relative to count data (Fig. 1.4). $\widehat{\Psi}$ and the multinomial $\hat{\lambda}$ estimate were positively correlated as well ($r = 0.78$).

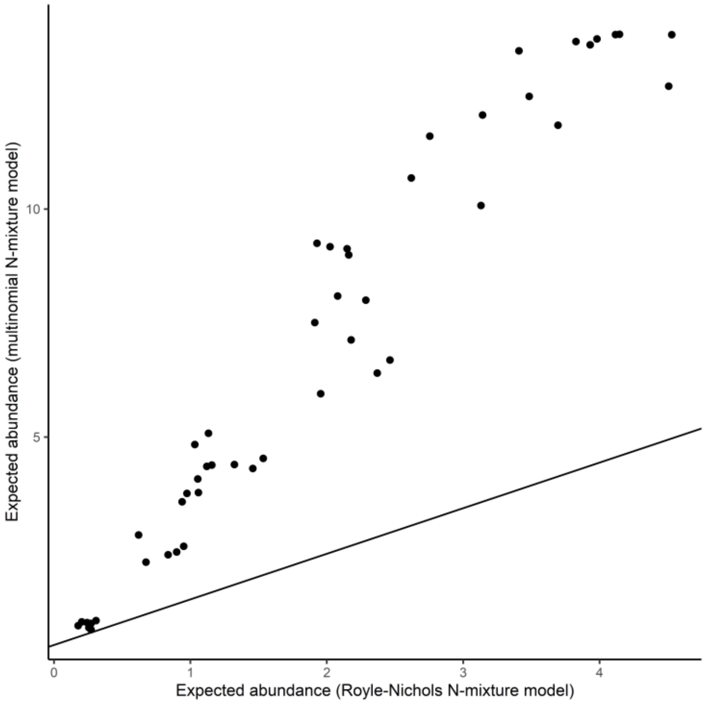

Figure 1.4. Estimated *Macrochelys temminckii* abundances for the best-fit Royle-Nichols *N*-mixture model (x-axis) and multinomial *N*-mixture model (y-axis) based on sampling efforts across the range of the species within Texas, United States. The relationship between estimated abundances is modeled linearly as $\hat{\lambda}_{i(multinomial)}$ = 0.44 + 3.308$\hat{\lambda}_{i(RN)}$ (R^2 = 0.94). The solid line depicts a slope of 1. Although both models allow similar inference by retaining the same covariates of abundance (latitude [additive and quadratic term] and longitude) and capturing relative abundance relationships between sites, the Royle-Nichols model consistently underestimated, with values often below counts of turtles actually observed (maximum estimated = 4.53, maximum observed = 17).

DISCUSSION

In eastern Texas, *M. temminckii* is likely to occupy the majority of large, permanent waters within watersheds it is known to inhabit, as indicated by the high mean occupancy probability. In these waters, variation in both occupancy and abundance of *M. temminckii* were better explained by geographic location and land cover than by local habitat variables. Occupancy probability and abundance increased towards median latitudes and within waters surrounded by highly-forested land, but influences of developed land, agricultural land, and wetland cover were not well-supported. Detection of the species was influenced by environmental and methodological heterogeneity, in addition to abundance, although despite the species' ectothermic physiology, temperature and date were not strong determinants. Furthermore, these results suggest that CPUE underestimated the extent of *M. temminckii* occurrence, and due to heterogeneity in detection probability across sites, would result in imprecise inferences if used as an index of relative abundance.

Determinants of detection probability

Survey efforts confirmed that environmental heterogeneity leads to variation in *M. temminckii* detectability. Specifically, these results indicate that when using CPUE as an abundance index, trapping under conditions of high flow will underestimate *M. temminckii* abundance. *Macrochelys temminckii* is predominantly benthic, with limbs adapted to gripping (Harrel et al. 1996b). During flood pulses, the species likely takes shelter in microhabitat refugia and reduces foraging to avoid being displaced downstream from core sites of occupancy (Sloan and Taylor 1987, Harrel et al. 1996a) and conserve energy that would be required for swimming. Furthermore, the increased water volume during these events may have diluted bait scent, and associated currents dispersed the scent downstream at a greater relative rate than would occur during low flow periods. These conditions would make it difficult for turtles downstream of traps to locate bait, as well as reduce the amount of time bait emitted scent. Jensen and Birkhead (2003) posited that lentic systems (i.e., waters with no flow) lead to lower detection probability of *M. temminckii* by reasoning that these systems cannot effectively disperse bait (Jensen and Birkhead 2003). However, this study demonstrates that the limited flow of lentic systems provides favorable physical conditions for detecting the species. In lotic systems, surveys should be conducted during low flow rates to maximize p of *M. temminckii*.

In accordance with the hypothesis that increased water volumes decrease trap effectiveness, increased trap spacing decreased detections of *M. temminckii*. Increasing space between traps will likely dilute bait scent, and reduce the probability of any turtle within a water body being near and entering a trap. Inter-trap distance is known to affect detection of other species. For example, in a study on *Panthera tigris* (tiger) abundance, Wegge et al. (2004) found that greater distances between camera traps reduced detections. However, trap spacing is more important for determining *M. temminckii* abundance than for confirming occupancy. Increasing trap density (i.e., reducing the area of aquatic habitat covered) in occupied habitat may be efficient for capturing more individuals, and I recommend that future survey efforts attempt to standardize and report inter-trap distances.

Detection of *M. temminckii* varied with lunar phase, with greater counts during new moons and lower counts near full moons. Relationships between lunar phase and nesting behavior of turtles are well-documented (Pinou et al. 2009, Bernardo and Plotkin 2007, Baldwin and Lofton 1959, Davis and Whiting 1977), but examinations of lunar influences on other behaviors (e.g., foraging activity) have revealed varying results. Foraging activity of Malaysian freshwater turtles exhibited no relationship with lunar phase (Jensen and Das 2008). However, Kot et al. (2009) noted lunar periodicity of marine turtle (*Carretta carretta* and *Dermochelys coriacea*) catch rate, with higher rates during full moons, and assumed this pattern resulted from greater foraging activity during bright nights. The opposite pattern observed from *M. temminckii* may result from its unique feeding methods. On bright nights, the species may more frequently ambush hunt for fishes using its vermiform lure. This postulation is contingent on fishes being able to visually discern lures better than in low-light conditions, and turtles being better able to see fishes (Drummond and Gordon 1979). Foraging efficiency of fishes has been documented to increase under increased irradiance (Fraser and Metcalfe 1997, McMahon and Holanov 1995). During low visibility nights (i.e., new moons), scavenging and active foraging may be a more effective method of food acquisition, which would explain increased detection probability near new moons. However, I observed *M. temminckii* entering traps diurnally on 3 occasions, indicating that scavenging takes place even under well-lit conditions (it should be noted that water turbidity is another factor that interacts with light in foraging dynamics of aquatic organisms; Benfield and Minello 1996). The quadratic relationship between *M. temminckii* detection probability and the lunar phase is robust (n = 141 surveys), but further examination of other capture datasets is needed to confirm or refute the relationship as a general pattern.

Within the range of conditions sampled, date nor temperature were reliable predictors of *M. temminckii* detectability. However, temperature affects both *M. temminckii* habitat selection and activity (Fitzgerald and Nelson 2011, Riedle et al. 2006). During temperature extremes of summer and winter, individuals occupy deeper water, and the species has been documented to cease feeding once water temperatures drop to 18°C (Riedle et al 2006). Due to these factors, Munscher et al. (2020) postulated that *M. temminckii* CPUE would increase if surveys were limited to times of year with milder temperatures. Johnson (2020) corroborated this with evidence that minimum air temperature and ordinal date influenced p in *M. temminckii* occupying a similar climate in Louisiana. In this study, however, individuals entered traps when surface water temperatures were at the minima recorded across all surveys: 13.3°C (early March 2021) and 14.2°C (early April 2021). Individuals also entered traps while surface temperature was 29.0°C (late June 2020), which was within one degree of the maximum temperature recorded in the study. Individuals were detected from March through September (the study period was contained between March and August in both years, with outlier surveys for two sites taking place in September and October 2020). Had I allocated survey efforts to late autumn and winter as well, greater ranges in date and temperature may have made the variables stronger predictors of *M. temminckii* detection probability.

The high mean *M. temminckii* detection probability (0.77) from the site occupancy model quantifies the efficacy of hoop trapping as a sampling method. However, other chelydrid hoop trap surveys have noted lower detection rates. *Chelydra serpentina* in Rhode Island and *M. temminckii* in Oklahoma and Louisiana exhibited mean detection probabilities of 0.40 (Buchanan et al. 2018) and 0.34 (Dreslik et al. 2017), respectively. The discrepancy in these estimates exemplifies the methodological and environmental subtleties that may influence whether turtles enter traps. Spatial variation in abundance is another important contributor to variation in *M. temminckii* detection, as evidenced by RN models tending to exhibit better fits than occupancy models. If Oklahoma and Louisiana surveys took place using similar methods (e.g., bait species of the same effectiveness) and environmental conditions (e.g., surveys occurred over similar regime of flow velocities) to those used here, the low estimates of *M. temminckii* detectability exhibited from the locales surveyed in these states may indicate lower mean abundance than sites surveyed in Texas.

Determinants of distributional patterns

CPUE did show a clear latitudinal pattern in relative abundance across the study area that was corroborated after quantifying false-negative error rate. This suggests that *M. temminckii* hoop trap surveys standardized only by use of CPUE (e.g., Folt and Godwin 2013, Huntzinger et al. 2019, King et al. 2016, Lescher et al. 2013) are capable of capturing general patterns in relative abundance, albeit with biases that arise from other sources of inter-survey and inter-site heterogeneity. Within the study area of eastern Texas, my findings provide little support that abundance of *M. temminckii* declines at longitudes closer to its western range edge in the state (Doherty et al. 2003). Because the western range boundary of *M. temminckii* is in Texas, a positive relationship between longitude and occurrence is inherent. The low magnitude of the relationship between longitude and occupancy and abundance likely resulted from the westerly reach of the Trinity watershed, where individuals have the ability to disperse to westerly longitudes that would encompass unoccupied watersheds (i.e., Brazos) at lower latitudes of the study region (Appendix 1).

Of the considered subwatershed variables, forest cover was the strongest predictor of *M. temminckii* occurrence and abundance, while decreased occurrence probability and abundance in developed and agricultural landscapes were not strongly supported. There are several reasons why forest cover within the study region could predict occurrence of the species well. First, the zone of high forest cover in eastern Texas could simply represent a climatic zone that delineates the range of *M. temminckii*. Forest cover in eastern Texas is associated with increased precipitation (Griffith et al. 2007), and it is expected that an obligate inhabitant of aquatic habitats would fare optimally under such conditions (Thompson et al. 2016). High precipitation and flooding in watersheds of this region increase potential for permanence and connectivity of the preferred habitat of *M.*

temminckii (Griffith et al. 2007), which would in turn increase its dispersal potential throughout aquatic habitats within watersheds it occurs.

There is also evidence *M. temminckii* benefits from the influences of watershed forest cover on aquatic habitat. Watershed land cover variables often capture variation of instream channel characteristics more accurately than do smaller-scale riparian zone land use variables (Richards et al. 1996, Wang et al. 2003, Allan et al. 1997), and large-scale forest cover is associated positively with instream habitat variables that are important to the ecology of *M. temminckii* (e.g., pooled areas and submerged cover; Wang et al. 1997, Riedle et al. 2006, Howey and Dinkelacker 2009). The species may also benefit from the protective buffers forest cover provides to bottomland swamps and water bodies (Booth et al. 2007). In general, aquatic communities benefit from increased forest within watersheds. Wang et al. (1997) noted a positive correlation between forested land cover and a fish assemblage index that quantified species richness. Similarly, species richness of macroinvertebrate and fish communities in North Carolina was higher in streams within forest-dominated watersheds than streams in watersheds with high urban cover (Crawford and Lenat 1989). Fish communities in less forested and more developed watersheds of the southeastern Appalachians exhibited lower numbers of endemic species and higher representation from more generalist taxa (Scott 2006). Turtle communities may benefit similarly from forested catchments through increased habitat heterogeneity and the greater array of food sources available. *Glyptemys insculpta* (wood turtle) abundance was positively associated with proportion of forest coverage in a 5km buffer around streams (Roberts et al. 2021). Similarly, *Clemmys guttata* (spotted turtle) occupancy probability in Rhode Island increased in wetlands buffered by forest (Buchanan et al. 2019). Considering known microhabitat preferences of *M. temminckii* and responses of other taxa to forested watersheds, it is likely that large-scale forest cover influences aquatic habitat in beneficial ways to the species, or correlates with instream characteristics that select for its occupancy and increased numbers. Furthermore, forest cover is inversely correlated with developed and agricultural land cover. Despite lower support for the *direct* negative impact of these cover types within the study area, decreases in forest cover driven by increases in developed and agricultural land may decrease habitat suitability and are predicted to result in a lower probability of the species' persistence.

Within the range of aquatic systems sampled in the study region, it appears that *M. temminckii* exhibits generalist tendencies regarding microhabitat use, as intercept-only submodels of abundance and occurrence explained variation better than measured instream habitat variables. This suggests the high associations between forest cover and *M. temminckii* occupancy and abundance are a result of shared climatic limitations. As mentioned above, however, there is substantial evidence that the species selects microhabitats that include features such as high canopy cover and submerged structure (Riedle et al. 2006, Howey and Dinkelacker 2009), so stream habitats that contain a greater amount of submerged structure and high canopy cover should be more suitable for occupancy and increased abundance. Indeed, a model showing a positive relationship between occupancy probability and these variables (albeit with high standard errors) did rank competitively with the intercept-only model. In Louisiana, proportion of woody debris and emergent vegetation also granted high degrees of uncertainty as predictors of *M. temminckii* occupancy (Johnson 2020).

The relative lack of explanatory ability of these variables in Texas and Louisiana is likely an artefact of trapping methodology. First, habitat variables were measured in the vicinity of each trap, so may not holistically quantify the abundance of suitable microhabitat within each site. Closely related to this supposition is the fact that turtles could be actively attracted to trap vicinities from other locations. When foraging or dispersing, *M. temminckii* may utilize typically unoccupied stretches (e.g., shallow, high-energy riffles; Ernst et al. 1994, Riedle et al. 2006) and be drawn into traps to feed regardless of adjacent microhabitat features.

Sinuosity and the human accessibility index measures do not pertain to microhabitat, however, so would not have been affected by these potential biases of detection via traps. This study did not provide evidence that increased channelization within the range of sinuosity I sampled negatively impacted turtle abundance. Nevertheless, even the lotic sites I visited with low sinuosity exhibited some sheltered low-energy pools and bends. Expanding the range of habitat types sampled (e.g., allocating representation of channelized urban habitats) may support the positive relationship between abundance and sinuosity (*sensu* Riedle et al. 2005).

That differences in abundance and occupancy were not captured by variation in local-scale habitat features may also indicate the distribution of the species depends on dispersal and connectivity between waters to a greater degree than on physical qualities of aquatic habitat. In Texas, the Colorado, Brazos, Trinity River lowlands consist of similar habitat intersecting the Blackland Prairie ecoregion (Griffith et al 2007), and natural populations of *M. temminckii* are only known to occur in the latter system (Rosenbaum et al. in press). The lack of the species in the former two drainages hints that dispersal barriers prevent its occurrence, given that the available habitat is similar to that in the Trinity watershed. Furthermore, individuals have been translocated and survived outside the native range of the species in unusual habitats such a reservoir in the desert of central Oregon (Oregon Department of Fish and Wildlife 2013), and a rocky stream in Korea (Koo et al. 2021). These observations of occupancy corroborate the ability of individuals to persist in a variety of physical habitats, but do not necessarily apply to population persistence.

In summary, *M. temminckii* is likely to occur in the majority of waters in the study area, and although it exhibits microhabitat preferences (Harrel et al. 1996), our methods and models incorporating local habitat variables are unable to provide substantial evidence that these variables select for the species across the study region. However, the relative explanatory ability of forest cover and instream habitat variables provide evidence the occurrence and abundance of the species in Texas may be determined by climatic factors or aquatic habitat characteristics over a large scale, and that its occupancy is limited by dispersal. Limitations of dispersal ability, climatic tolerance, and physical habitat suitability are not mutually exclusive means of determining the observed patterns in this study.

In general, occupancy and abundance are positively related, and the occupancy status of an area conveys rudimentary abundance information ($N_i > 0$) (Gaston et al. 2002, Kéry and Royle 2016). The high correlation between estimates of occupancy and abundance in this study reflects this relationship, as do congruencies in the relative explanatory ability of geographic location and subwatershed land cover types in model sets of both occupancy and abundance. This research revealed that using only detection/nondetection datasets can lead to similar inferences as those incorporating count data, as shown in other studies that simultaneously apply models of occurrence and abundance (Linden et al. 2017, Ward et al. 2017, Doré et al. 2011). However, land cover variables had a greater apparent effect on occupancy than abundance. For example, forest cover did not describe heterogeneity in abundance to the same degree it did occurrence, as expressed by the low relative Akaike weight of the RN best-fit subwatershed model and lower explanatory ability for count data. These differences provide evidence that *M. temminckii* abundance is driven by additional environmental variables in addition to those dictating distribution (Ward et al. 2017).

Management Implications

Binary detection data underestimated abundance of *M. temminckii*, so the Royle-Nichols model is best to use only for relative abundance inferences. Because count data more precisely capture variation in abundance and detectability across sites, they should be used to optimize monitoring efforts of long-lived and persistent animals, such as *M. temminckii*. For such species, occupancy surveys— even if separated by decades— will be ineffective at detecting population declines where the same few individuals are persisting even after recruitment has ceased (Reed et al. 2002, Ward et al. 2017). In hoop trap surveys, many fish and turtle species are easily detectable, counts are collected passively, and individuals can be uniquely marked to prevent recount, which are all conducive to abundance monitoring under a removal sampling framework.

Surveys of *M. temminckii* are in great need of a uniform standardization in methodology, as well as implementation of analyses that account for uncontrollable (i.e., environmental) detection heterogeneity. Standardization would allow cross-study comparisons of relative abundance without requiring assumptions that are unlikely to be met. Additionally quantifying false-negative error rate in estimates would grant much more accurate comparative inference than CPUE provides.

The overall estimated density of 8 individuals/channel km across eastern Texas is lower than has been estimated from long-term population studies in Georgia (14 individuals/km; Folt et al. 2016) and Oklahoma (28 and 68 individuals/km; Riedle et al. 2008b). However, the estimate in this study is fundamentally different from these studies, so is not directly comparable. Specifically, it is an average over all sites in the study area (across the “meta-population” *sensu* Kéry and Royle 2016), even those where the species is estimated to be absent, as opposed to an estimate based on intensive sampling of one population. There are currently no available abundance indices from other regions to compare the value provided by this study aside from CPUE. Subsequent large-scale studies of the species that calculate mean abundance across sites would enable reliable comparisons across states in which the species occurs. This would streamline holistic, range-wide assessments of the species with minimal confounding biases between studies.

For management efforts with the goal of confirming the presence or absence of *M. temminckii* at specific locations, one should conduct 3 surveys per site to achieve 95% confidence of true absence, conditional upon the methods utilized in this study and average survey conditions. Similarly, to estimate density at a location, 9 surveys (replicating the methods of this study) should be conducted for 95% confidence all individuals available for potential capture within the trapping period are detected. This method will be of greatest use for relatively closed systems such as oxbows, where the assumption of closure is more likely to be met for the duration of the survey period.

Although no range contraction of *M. temminckii* has been documented in Texas, the lack of detections and lower predicted abundance within the Red River watershed leaves the status of the species within the northern extent of its Texas range from Red River to Grayson Counties nebulous. Notably, many subwatersheds surrounding the Red River where I failed to detect the species have high forest cover. Because this region contains suitable landcover and is within a watershed the species is known to occur, it is cause for concern that no individuals have been detected there, and indicates unmodeled factors are decreasing occupancy and abundance (relative to other watersheds) throughout the area. Furthermore, based on forest cover proportions, individuals may be present in the northwestern extent of the Trinity watershed where targeted surveys for the species have yet to occur. Future studies should also examine the distribution of the species in this region, where several unmodeled factors may preclude its presence, including a more arid environment and network of impoundments. Evidence for the influence of subwatershed forest cover on *M. temminckii* occurrence and abundance, corroborated by the effects of subwatershed cover on fish communities reported from other studies, highlight a need to consider the effects watershed influences will have on aquatic systems when managing land. Because the species has a high probability of occurrence in undeveloped catchments with moderate to high forest cover, these sites should be prioritized for conservation throughout the range of the species, and maintaining such areas will help ensure its persistence.

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Mercury Contamination of Alligator Snapping Turtles (*Macrochelys temminckii*) in Texas

INTRODUCTION

Of the anthropogenic contaminants in aquatic systems, mercury (Hg) is particularly noteworthy due to its pervasive occurrence across the globe (Menounou and Presley 2003, Chen and Driscoll 2018) and its propensity to contaminate and accumulate in biota once introduced to such systems (Driscoll et al. 2007). At sufficient concentrations, Hg is teratogenic, embryotoxic, and neurotoxic to exposed animals (Wiener et al. 2003, Hopkins et al. 2013a), making it a contaminant of significant epidemiological and ecological concern (Ekino et al. 2007, Chen and Driscoll 2018). Variation in Hg levels across the environment is dependent on a multitude of abiotic and biotic variables that influence deposition and accumulation (Wiener et al. 2003).

The majority of Hg in the environment and biota has been made available for biogeochemical cycling through anthropogenic activity occurring since the mid-1800s (Menounou and Presley 2003, Lindberg et al. 2007). In the United States, airborne emissions from coal-fired power plants (CFPPs) are now the predominant source of environmental Hg (Evers et al. 2007). Despite the high atmospheric mobility of Hg (Driscoll et al. 2007, Chumchal and Drenner 2015, Li et al. 2020) and its ubiquity across the globe (Chen and Driscoll 2018), it often occurs at lower concentrations as distance from point sources increases (Alonso et al. 2003, Sullivan et al. 2006, Sackett et al. 2010, Martin and Nanos 2016).

Variation in land cover also influences variation in both Hg deposition rate and bioaccumulation. Forest cover and deposition are positively associated, as tree stomata uptake atmospheric Hg, after which it is deposited into the soil through litterfall (Grigal 2002, Driscoll et al. 2007). Because of this, watersheds with high forest cover contain aquatic biota with high Hg concentrations (Drenner et al. 2013). Once Hg is deposited to the soil, anaerobic bacteria that inhabit anoxic sediments of aquatic systems methylate mercury into an organic form (methylmercury or MeHg) that is capable of trophically magnifying and accumulating within individual consumers (Driscoll et al. 2007, Chumchal and Hambright 2009). Wetlands and frequent flood pulses facilitate decomposition and provide reducing soil conditions that in turn stimulate Hg methylation (Brumbaugh et al. 2001, Wiener et al. 2003), resulting in high Hg levels in aquatic organisms. Creation of reservoirs also facilitates decomposition and flooding, and subsequently increases Hg concentrations of organisms in these newly formed habitats (Bodaly et al. 1997, Paterson et al. 1998).

Following environmental exposure to Hg determined by these extrinsic variables, concentrations within exposed organisms depend on a variety of intrinsic factors. Because Hg biomagnifies, taxa and individuals occupying high trophic positions tend to exhibit high concentrations (Montaña et al 2021), with food sources high in Hg leading to concentrations orders of magnitude higher in their consumers (Monteiro et al. 1998). The amount of Hg any individual will accumulate is also dependent on physiology (i.e., uptake rates and elimination rates; Madenjian et al. 2016), size, and age. Age and size are often correlated with ontogenetic dietary shifts, and therefore can correlate with variation in biomagnification (Szczebak and Taylor 2011), and influence bioaccumulation (Brasso et al. 2014). Longer-lived individuals are potentially exposed to more Hg through time (Burger and Gochfeld 2007), and may contain elevated concentrations if their Hg elimination rate is lower than their uptake rate.

Because many interacting extrinsic and intrinsic factors influence the concentration of Hg in the environment and across species, predicting specific degrees of contamination is difficult. The most efficient way of monitoring impacts of Hg contamination is to directly assess concentrations within organisms (Hannappel et al. 2021). Of the vertebrates, Hg contamination and its toxic effects in fish, bird, and mammal taxa are well-documented (Wiener et al. 2003), whereas understanding of Hg contamination in aquatic reptiles is relatively limited (Rainwater et al. 2005, Schneider et al. 2013, Haskins et al. 2019). However, recent studies on several aquatic turtle species have revealed that they span a wide range of Hg concentrations and experience deleterious effects from the metal at high concentrations (Schneider et al. 2013, Hopkins et al. 2013a).

Turtles typically feed across multiple trophic levels, but those species that occupy higher trophic positions have higher total mercury (THg) concentrations (Bergeron et al. 2007). Furthermore, under some circumstances, larger turtles have relatively high THg concentrations, suggesting bioaccumulation (Schneider et al. 2009, Hopkins et al. 2013b), but this pattern is not always observed (Golet and Haines 2001, Schneider et al. 2010, Turnquist et al. 2011, Hopkins et al. 2013b). Studies on *Chelydra serpentina* (common snapping turtle) indicate that high concentrations resulting from vertical transmission lower reproductive success and cause aberrant hatchling behavior (Hopkins et al. 2013a, Landler et al. 2017).

Macrochelys temminckii (alligator snapping turtle) is a close relative of *C. serpentina* that is widespread in the southeastern United States. It is currently proposed for listing as a Threatened species by the United States Fish and Wildlife Service (Environmental Conservation Online System 2021), in part due to historical commercial harvests and contemporary recreational harvest pressure that is legal in Mississippi and Louisiana (Environmental Conservation Online System 2021). The Hg exposure levels of *M. temminckii* are currently unknown, as is the potential risk to humans that consume the species.

In this study, I assessed THg concentrations of *M. temminckii* sampled from aquatic ecosystems throughout eastern Texas, and hypothesized that body size and extrinsic factors (habitat and landscape features) would correlate with Hg concentrations. The high forest cover, density of impoundments, and wetland habitat of this region are conducive to Hg deposition and methylation (Drenner et al. 2013), and many of its waters have fish consumption advisories due to high Hg levels (Texas Parks and Wildlife 2022). I predicted that increased forest and wetland coverage surrounding sampled sites would provide conditions for elevated THg concentrations in *M. temminckii*, and that greater distance from headwaters would increase potential for sites to accumulate allochthonous THg and in turn expose the species to higher concentrations. Furthermore, coal-fired power plants in the region act as potential point sources of atmospheric Hg; therefore, I hypothesized that concentrations would depend on proximity to these plants. Because *M. temminckii* has a varied diet that includes piscivorous fishes (Elsey 2006), and its close relative *C. serpentina* is often contaminated with relatively high THg concentrations (Turnquist et al. 2011), I predicted that *M. temminckii* would possess elevated internal THg relative to sediment and fish sampled from the same locations. Because the longevity of the species may predispose it to bioaccumulation risk (McIntyre and Beauchamp 2007), I predicted that larger (and presumably older) individuals would exhibit the greatest THg burdens analogous to patterns exhibited by certain fish species (Burger and Gochfeld 2007, Wiener et al. 2003). Elucidating the degree of contamination in *M. temminckii* enables inference of health risks to the species and its consumers, which may in turn provide valuable information to contextualize its conservation needs.

METHODS

Study Area

Surveys occurred within the major watersheds of eastern Texas and included the San Jacinto, Trinity, Neches, Sabine, and the Mississippi watersheds. The Mississippi watershed contains the Red, Sulphur, and Cypress watersheds, which confluence in Louisiana, while the other watersheds are contained in Texas and drain directly into the Gulf of Mexico (Appendix 1). Within these watersheds, I surveyed for *M. temminckii* in 31 waterbodies of different habitat types including reservoirs, oxbows, sloughs, river mainstems, and tributaries. These sites were often connected to extensive bottomland and herbaceous wetland habitat conducive to mercury methylation. I collected *M. temminckii* tissue from all sites where the species was successfully detected (*n* = 14 sites), with at least one site representing each of the major watersheds surveyed.

Sampling methods

I deployed single-funnel, finger-throated, four-hoop traps (hoop diameter = 1.2 m; mesh size = 2.54 cm) to sample *M. temminckii*. Each trap was baited with fish held within a holding canister (constructed from 7.6 cm x 30.5 cm PVC pipe with 36 1.3 cm-diameter holes) suspended from the rear hoop of each trap. *Cyprinus carpio* was the predominant bait species used, but I occasionally supplemented this with *Ictiobus* spp., *Morone* spp., *Aplodinotus grunniens*, and *Ictalurus* spp.

Site sampling efforts were standardized to 45 trap nights (15 hoop traps deployed for 3 consecutive nights). However, during 7 site visits, logistical constraints such as flood events and trap theft resulted in fewer nights of sampling and fewer deployed hoop traps. I preferentially deployed traps upstream of aquatic structures, undercuts, or low energy pools, as these areas provide microhabitat preferred by *M. temminckii* (Harrel et al. 1996).

I checked traps and removed captured animals every morning (approximately every 24hr) during sampling efforts. I measured midline straight carapace length (body size) and mass of all captured *M. temminckii* with tree calipers (*sensu* Method D of Iverson and Lewis 2018) and a hanging digital scale, respectively. Following measurements of each *M. temminckii* greater than 5kg in body mass, I used a single-use 6mm diameter biopsy punch to procure a skeletal muscle sample from the ventrolateral aspect of the tail, posterior from the cloacal aperture (Dutton 1995, St. Andrews 2021). Acquiring muscle first required rotation of the biopsy punch through dermal and adipose tissue. After removing superficial tissue and reaching muscle, the punch and isopropanol-sterilized forceps were used to separate and remove a small muscle sample. Thick adipose deposits prevented muscle sampling from two large adult males. Average muscle sample mass was 109.3mg ± 4.3mg (mean ± standard error [SE]; $n = 84$). Wounds were immediately treated with povidine iodine, and pressure was applied to stanch bleeding.

The tails of individuals less than 5kg in body mass ($n = 7$) were too narrow in diameter to allow biopsy of muscle. On these individuals, I sampled 0.5 cm in length from the tail terminus with a single-use biopsy punch. Tail clips were considered as muscle samples for summary statistics, but mean values of muscle samples alone were also calculated. The tail sampling protocol involved the same disinfection method as muscle acquisition. After sampling either muscle or tail-clippings from individuals, I sampled 2-3 nail clippings from the hind left limb of 91 turtles using isopropanol-sterilized wire cutters. All sampled turtles (*n* = 93) were released at their points of capture.

In order to assess the degree that *M. temminckii* THg concentrations depended on site-specific exposure, and to infer whether biomagnification was occurring in these systems, I collected additional samples for Hg analysis. While setting traps, I obtained three 15 mL surficial sediment samples per site. Each of the 3 samples was selected to be representative of substrate heterogeneity within each trapped area (e.g., if one section within the trapped area had a substrate predominantly consisting of humus, while another section consisted largely of sand, I acquired samples of both sediment types). Additionally, when available, I collected one *Pomoxis annularis* (white crappie) or *P. nigromaculatus* (black crappie) from each site to compare their THg concentrations with those of *M. temminckii*. These fish species are abundant throughout the Texas range of *M. temminckii*, and can provide insight on THg levels of its food sources (Elsey 2006). All field samples (sediment, *Pomoxis*, and *M. temminckii* tissues) were stored on ice, and at the conclusion of surveys were retained at -20 °C in a storage freezer until further processing.

In a laboratory setting, three samples of axial muscle were taken from each *Pomoxis* specimen. The average mass of fish muscle samples was 431.3 ± 14.4 mg (mean ± SE; *n* = 31). Following this procedure, I recorded the wet weight (ww) of all *Pomoxis* and *M. temminckii* samples to the nearest 0.1mg. These samples were rinsed with deionized water to remove any sediment or particulate residue that remained from field collection. All samples were then dried at 60°C for 48 hours to remove water, after which dry weights (dw) were recorded, which enabled calculation of water percentages within each muscle sample.

Mercury Analysis

I analyzed THg concentrations of sediment, nail, and muscle samples using a direct mercury analyzer (DMA-80; Milestone, Inc., Monroe, Connecticut). This instrument thermally decomposes samples and Hg in resulting gas is collected via gold amalgamation and quantified with atomic absorption spectroscopy (U.S. EPA Method 7473). Quality assurance included the analysis of approximately 3 blank samples and 4 reference samples at regular intervals between every 33 field-collected samples, and duplicate samples. I used two materials from the National Research Council of Canada as references for samples with relatively low and relatively high amounts of mercury, respectively: DORM-4 (fish protein) and PACS-2 (marine sediment). The mean (± SE) percentage recovery of references was 97.7 ± 1.70%. Blank samples contained 0.32 ± 0.057ng THg with a range of 0.0ng - 1.0ng (*n* = 21). I analyzed duplicates of approximately every 20 samples. Average (± SE) percentage different between duplicate samples was 21.1 ± 5.7% (range 0.1 – 85.0 %; *n* = 22). Discrepant duplicate concentrations were exhibited by *M. temminckii* muscle samples and are likely attributable to differences in lipid concentrations between duplicates.

Habitat Variables

Within a 5 m radius of each trap, I recorded the presence or absence of submerged and emergent vegetation. Additionally, using a concave spherical densiometer, I calculated proportion of canopy cover above each trap opening *sensu* Strickler (1959), with 4 readings taken orthogonal to each other. All measures collected at each trap were averaged for a representative per-site value of canopy coverage and aquatic vegetation coverage.

I acquired data for landscape-scale variables with ArcGIS Desktop 10.7.1 (ESRI, Redlands, CA, USA). All georeferenced data used with the software were projected to Texas Statewide Mapping System of the North American Datum (NAD) of 1983. The landscapes around each sample site where *M. temminckii* were sampled were limited to USGS subwatersheds (12-digit Hydrologic Unit) defined by the Watershed Boundary Dataset of USGS (USGS 2020). Subwatershed boundaries are delineated by surface water flow and topography, so define biologically relevant landscape units (USGS 2009).

Using land cover data from the conterminous United States National Land Cover Database (NLCD 2019) (Dewitz and USGS 2021), I calculated the proportions of open water cover, total wetland cover (the aggregation of NLCD-defined woody and emergent herbaceous wetlands), deciduous forest cover, evergreen forest cover, total forest cover (the aggregation of NLCD-defined deciduous, evergreen, and mixed forest cover), and total developed land cover (the aggregation of all NLCD-defined developed categories) within each subwatershed of *M. temminckii* sampling. Because coal-fired power plants (CFPPs) are potential point sources of environmental Hg, I obtained locations of these plants in Texas, Oklahoma, Louisiana, and Arkansas (Energy Information Administration 2021). The linear distance of the nearest coal-fired power plant to sample sites was used as a covariate of *M. temminckii* THg concentration, as was the distance from sampling sites to headwater location (determined from the National Hydrography Dataset [USGS 2020]).

Statistical Analyses

I first calculated summary statistics for THg concentrations within each sample type to infer whether *M. temminckii* exhibits higher concentrations than *Pomoxis* and sediment samples, and assess potential health risk and Hg exposure to humans that consume it. To examine the degree to which THg in different matrices correlated by site, I calculated pairwise Pearson's correlation coefficients (*r*) between the average sediment THg concentration of each site, the average *Pomoxis* muscle THg concentration of each site, and individual *M. temminckii* THg. To assess the degree to which nail samples were capable of predicting skeletal muscle concentrations in turtles, I regressed *M. temminckii* nail THg concentrations against respective muscle THg concentrations. Then, I used ANOVA to ascertain differences between nail THg concentrations between the 5 major watersheds sampled, followed by a Tukey post hoc test to determine which watershed(s) had statistically different concentrations. For comparison with other studies that examine turtle THg burdens, I conducted linear regression with the body size of individuals as predictor of their muscle THg concentrations. The data in both analyses met model assumptions. Nail THg concentration was used as the dependent variable in subsequent statistical analyses (see below) because associated reference samples had a closer percentage recovery to 100%.

I formulated a series of 15 general linear models in accordance with hypotheses regarding which large-scale and local-scale environmental variables, and their interactions with other variables including body size, would best predict *M. temminckii* THg concentrations (Table 2.1, Table 2.3). Prior to fitting models, all independent variables were z-standardized for ease of coefficient interpretation, and collinearity was assessed with Pearson's correlation coefficients (r) to ensure no covariates with pairwise $r \geq 0.5$ occurred in the same model. Relative model fit was inferred with an information theoretic perspective using likelihood, Akaike's Information Criterion corrected for small sample size (AIC_c), and Akaike weights (w_i) (Burnham and Anderson 2002). All statistical analyses were conducted using statistical software R 4.0.5 (R Core Team 2021). Model selection was computed with the R package *AICcmodavg* (Mazzerole 2020).

Table 2.1. Extrinsic and intrinsic covariates hypothesized to predict total mercury (THg) concentrations in *Macrochelys temminckii*.

	Covariate name	**Description**
watershed cover and large-scale covariates	open water	Proportion of NLCD 19-defined open water cover within the USGS subwatershed containing the survey site.
	forest cover	Combined proportion of NLCD 19-defined deciduous forest, evergreen forest, and mixed forest cover within the USGS subwatershed containing the survey site.
	wetland cover	Combined proportion of NLCD 19-defined woody wetlands and emergent herbaceous wetlands cover within the USGS subwatershed containing the survey site.
	CFPP	The linear distance from the sampling location to the nearest coal-fired power plant (CFPP).
	headwater	The linear distance from sampling location to the headwaters sourcing the aquatic system sampled.
	watershed	Identity of watershed sampled from (Mississippi, Sabine, Neches, Trinity, or San Jacinto).
Local habitat covariates	veg	Proportion of traps within a site where submerged or emergent vegetation was observed.
	debris	Proportion of traps within a site where emergent and/or submerged woody debris was observed.
	canopy	Average canopy cover percentage above traps set at a site.
intrinsic variable	body size	*M. temminckii* midline straight carapace length (*sensu* Iverson and Lewis 2018 Method D).

RESULTS

Of the four sample matrices, sediment exhibited the lowest mean THg concentration, followed by *Pomoxis* muscle, *M. temminckii* muscle, and *M. temminckii* nail (Table 2.2). On average, *M. temminckii* and *Pomoxis* muscle samples consisted of 72.6% and 78.9% water by mass, respectively. *Pomoxis* samples averaged 0.235 ± 0.029 ppm THg ww, while *M. temminckii* muscle and tail averaged 0.312 ± 0.017 ppm THg ww. *Macrochelys temminckii* muscle samples alone averaged 0.315 ± 0.018 ppm THg ww. Average sediment concentrations at each site exhibited no apparent correlation with concentrations of *M. temminckii* nail (*r* = 0.21) and muscle (*r* = -0.04) samples. *Pomoxis* muscle THg concentrations exhibited stronger positive relationships with average site sediment THg concentrations (*r* = 0.55), *M. temminckii* muscle THg concentrations (*r* = 0.52), and *M. temminckii* nail THg concentrations (*r* = 0.60).

Table 2.2. Dry weight (dw) concentrations of total mercury (THg) in sediment, *Pomoxis*, and *Macrochelys temminckii* tissues sampled across eastern Texas. *M. temminckii* keratin (nail) contained the highest THg burdens, and muscle samples from both species reflected similar dw concentrations.

	Sediment	***Pomoxis* muscle**	***M. temminckii* muscle/tail**	***M. temminckii* nail**
Sample size	36	31	91 (84 muscle, 7 tail)	91
THg ppm dw (mean ± SE)	0.023 ± 0.003	1.146 ± 0.150	1.160 ± 0.075	4.212 ± 0.244
range	0.003 - 0.0655	0.177 - 3.352	0.147 - 4.011	0.228 - 15.615

Macrochelys temminckii muscle THg concentrations were predictive of nail THg concentrations (Fig. 2.1). On average, nail samples contained 3.63 times more THg by concentration than muscle samples (dw), and the modeled relationship indicates that on average, every 4.33 ppm increase in nail THg concentration corresponds to a 1 ppm increase in muscle THg concentration. Nail THg concentrations differed among watersheds ($F_{4,86}$ = 3.21, P = 0.016), with the Mississippi watershed exhibiting statistically higher concentrations than those in Sabine watershed by 3.198 ± 0.897 ppm (mean ± SE; P = 0.005; Fig. 2.2). Mean (± SE) nail concentrations were 4.509 ± 0.720 ppm in the San Jacinto, 4.209 ± 0.329 ppm in the Trinity, 3.992 ± 0.516 ppm in the Neches, 2.998 ± 0.173 ppm in the Sabine, and 6.147 ± 0.503 ppm in the Mississippi. *Macrochelys temminckii* body muscle THg concentrations increased with increasing body size, but this relationship was not significant (Fig 3).

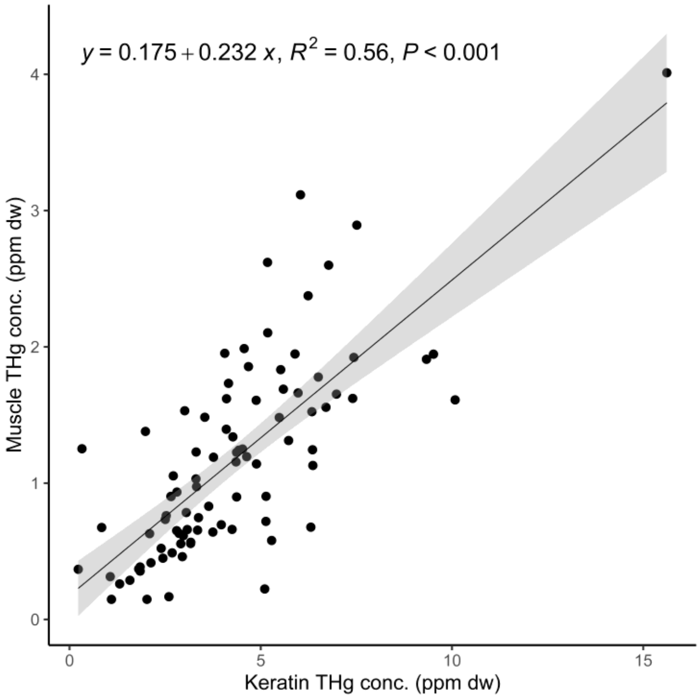

Figure 2.1. Linear regression of nail (i.e., keratin; x-axis) THg concentration as a predictor of skeletal muscle THg concentration (y-axis) with samples from *n* = 87 *Macrochelys temminckii*. The 95% CIs of the intercept and coefficient were -0.366 – 0.387 and 0.188 – 0.275, respectively.

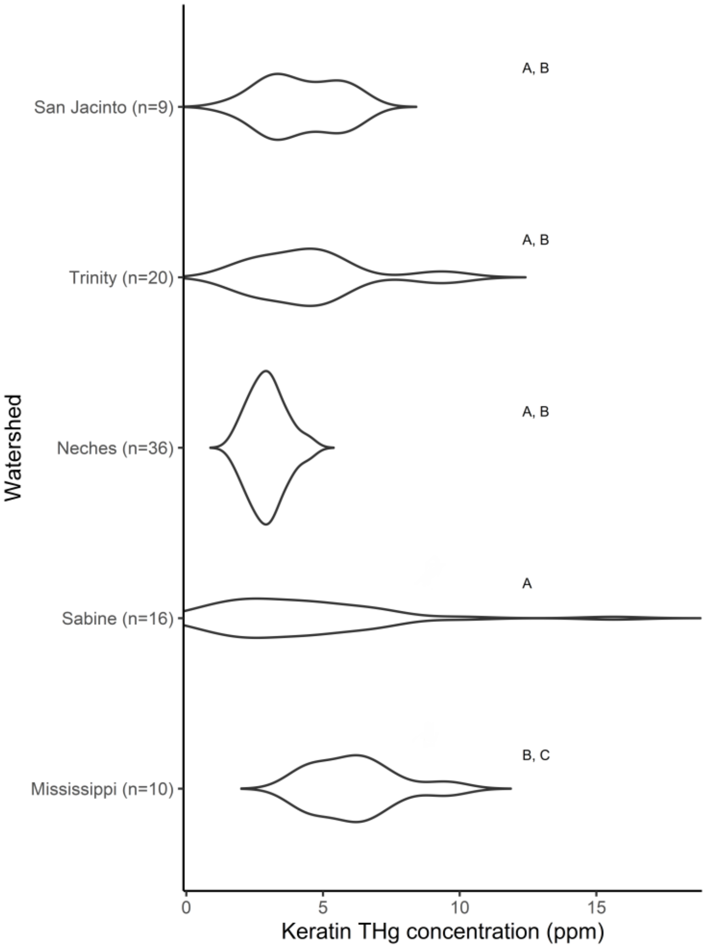

Figure 2.2. Distributions of *Macrochelys temminckii* nail (*n* = 91) total mercury (THg) concentrations (x-axis) throughout the 5 watersheds sampled (y-axis). Turtles in waters of the Mississippi watershed (i.e., tributaries of the Red, Sulphur, and Cypress Rivers) had statistically greater concentrations than turtles in the Sabine watershed. A shared letter between watersheds indicates no statistical difference in mean THg concentration.

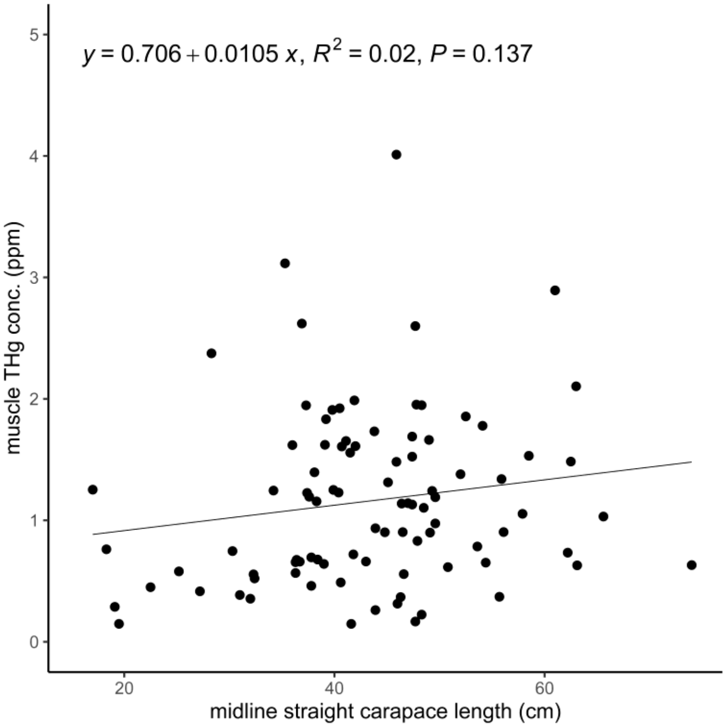

Figure 2.3. Linear regression of *Macrochelys temminckii* body size (midline straight carapace length; x-axis) as a predictor of skeletal muscle total mercury (THg) concentration (y-axis) with samples from *n* = 91 individuals. The 95% CIs of the intercept and coefficient were 0.088 – 1.324 and -0.003 – 0.024, respectively.

Watershed landcover types alone were poor predictors of *M. temminckii* THg concentrations (Table 2.3). Instead, the effects of total wetland, total forest cover, and local canopy cover on THg concentrations were contingent upon the distance to the nearest coal-fired power plant, as indicated by the higher Akaike weights (w_i) of models with interactive effects (Table 2.3). Furthermore, local habitat variation in canopy and aquatic vegetation coverage were stronger determinants of THg concentration than additive landcover effects alone. Body size was not predictive of THg concentrations even after controlling for potential variation in its effects arising from dependence on watershed cover types, location, and distance to nearest coal-fired power plant (Table 2.3).

Distance to the nearest coal-fired power plant had a negligible effect on *M. temminckii* THg concentrations at mean values of subwatershed forest cover and local canopy cover (Table 2.4). However, at mean values of subwatershed wetland cover and local canopy cover, this variable exhibited a strong negative relationship with THg concentrations (Table 2.4). THg concentration in *M. temminckii* increased with wetland cover and proximity to coal-fired power plants, but wetland cover had less of an effect closer to coal-fired power plants, and distance from coal-fired power plants had a weaker effect on THg concentrations in waters with high wetland cover (Table 2.4). However, the positive effects of local canopy cover and subwatershed forest cover were more pronounced with greater proximity to coal-fired power plants. The effects of canopy cover were corroborated by both competitive AIC_c models (Table 2.4).

Table 2.3. The relative fit of regression models assessed to weigh evidence of various hypotheses regarding environmental and intrinsic variables of total mercury (THg concentrations) in *Macrochelys temminckii.* Bolded models are within the 95% confidence set (i.e., cumulative Akaike weight [w_i] of at least 0.95). For definitions of covariate meanings, see Table 2.1. *K* and LL denote number of parameters and log-likelihood, respectively. Interactive effects (noted with “*”) between potential point sources of environmental mercury (i.e., distance to nearest coal-fired power plant) and physical characteristics of the environment on large and local spatial scales were the best predictors of mercury levels in the species.

Regression Model	*K*	AICc	Δ AIC_c	w_i	LL
CFPP * forest + CFPP * canopy	**7**	**1,643.61**	**0.00**	**0.58**	**-814.13**
CFPP * wetland + CFPP * canopy	**7**	**1,644.39**	**0.78**	**0.39**	**-814.52**
canopy + veg	4	1,649.80	6.18	0.03	-820.67
CFPP	3	1,661.87	18.26	0.00	-827.80
forest * CFPP * wetland	9	1,662.27	18.66	0.00	-821.02
CFPP * wetland	5	1,662.57	18.96	0.00	-825.93
CFPP + headwater	5	1,665.09	21.47	0.00	-827.19
body size * CFPP	5	1,665.75	22.14	0.00	-827.52
forest * wetland	5	1,667.26	23.65	0.00	-828.28
forest * wetland + open water	6	1,669.44	25.83	0.00	-828.22
body size * watershed	11	1,671.74	28.13	0.00	-823.20
intercept	2	1,672.59	28.98	0.00	-834.23
wetland + open water	4	1,675.67	32.06	0.00	-833.60
forest + wetland	4	1,676.50	32.89	0.00	-834.02
forest + wetland + open water	5	1,677.86	34.25	0.00	-833.58

Table 2.4. Parameter estimates for the two most parsimonious models of *Macrochelys temminckii* THg concentrations in eastern Texas. See Table 2.1 for definitions of covariates associated with parameters. Asterisks (*) on standard errors indicate 95% confidence intervals that do not overlap zero.

Top model			**Competitive model**		
Parameter	Estimate	SE	Parameter	Estimate	SE
Intercept	3659.3	282.3*	Intercept	4002.2	241.6*
CFPP	184.4	286.8	CFPP	-690.0	234.4*
Forest	884.1	275.8*	Wetland	911.0	252.1*
Canopy	2340.2	455.4*	Canopy	1411.2	330.2*
Interaction (CFPP and Forest)	-386.1	230.2	Interaction (CFPP and Wetland)	340.0	204.8
Interaction (CFPP and Canopy)	-1174.7	405.5*	Interaction (CFPP and Canopy)	-246.7	284.1

DISCUSSION

Macrochelys temminckii in Texas are contaminated with THg at concentrations within the range of those documented from other turtle species (Schneider et al. 2010). The species exhibits spatial variation in THg concentrations, as indicated by the higher concentrations within the greater Mississippi watershed. Variation in these values was best-predicted by a combination of local habitat variables, watershed land cover variables, and the distance to coal-fired power plants. However, across the Texas range of the species, larger turtles did not accumulate significantly more THg than smaller turtles.

The increase in average THg concentrations from sediment samples to *Pomoxis* samples and *M. temminckii* samples are consistent with *M. temminckii* occupying a higher trophic position than *Pomoxis* and experiencing greater THg burdens due to trophic biomagnification. Furthermore, the positive correlation between *Pomoxis* and *M. temminckii* samples occupying the same sites provides evidence that organismal THg concentrations are influenced by site-specific variables. However, local sediment THg concentrations were not correlated with those in *M. temminckii.* The relationship between THg in sediment and organisms is mediated by rate of conversion of inorganic mercury to methylmercury (Kannan et al. 1998) so the nature of the relationship may vary across locations. For example, in the northeastern United States, a non-significant correlation between sediment and fish was documented, and attributed to site-specific characteristics (e.g., increased organic matter and vegetation typical of wetland habitats) influencing methylation rates (Sorensen et al. 1990).

The predictive ability of forest cover and wetland cover, and the positive association of these variables with THg concentrations in *M. temminckii*, corroborate findings in other studies that have examined watershed-scale influences on organismal THg concentrations. Spatial differences in concentrations in other taxa also result from environmental influences on the element's biogeochemical cycling (Wiener et al. 2003). Across the southeastern United States, Hg concentrations in piscivorous fish were well-predicted by coniferous forest coverage (Drenner et al. 2013), and concentrations in fish communities throughout the United States were greater in waters exhibiting greater proportions of watershed wetland cover (Ward et al. 2010, St. Louis et al. 2001, Brumbaugh et al 2001). A similar correlation has been documented between keratin THg concentrations of *C. serpentina* and watershed forest cover. (Turnquist et al. 2011).

Local measures of canopy cover and proportion of aquatic vegetation are indicative of local forested and wetland habitats, respectively, and provide support for the influence of forests and wetlands on Hg deposition and methylation at small spatial scales. Among the variables considered, canopy cover was the best predictive covariate of THg in *M. temminckii*. This association is supported by the documented ability of leaf coverage and increased litterfall to increase local THg contamination (St. Louis et al. 2001, Bushey et al. 2008, Witt et al. 2009, Ward et al. 2010).

However, habitat variables determining THg accumulation are likely mediated by amount of the contaminant available for input. Patterns across the study area provide evidence that the effect of canopy cover depends on site distance from coal-fired power plants. The greater positive influence of canopy on THg when in proximity to power plants is expected, given that these industrial plants are likely major sources of THg in the region (Evers et al. 2007), and that atmospheric deposition can be greater in areas adjacent to coal-fired power plants (Menounou and Presley 2003, Sackett et al. 2010). The relationship observed in eastern Texas suggests that more Hg is made available for deposition (and subsequently accumulation in *M. temminckii*) through greater canopy litterfall. Similarly, Alonso et al. (2003) observed an inverse correlation between distance from atmospheric sources and THg concentrations in terrestrial biota.

As was the case for canopy cover, the effects of watershed-scale wetland and forest cover were also conditional on distance to the nearest coal-fired power plant. However, these interactions were not as strong a predictor of *M. temminckii* THg concentrations as the interaction between canopy cover and distance to coal-fired power plant. Power plants exhibited a similar pattern of influence on the effects of forest cover as they did for canopy cover. These interactions suggest that Hg deposition rate and intake in forests depends on a gradient in atmospheric Hg concentrations (St. Louis et al. 2001, Bushey et al. 2008, Witt et al. 2009, Ward et al. 2010) with greater deposition in forests exposed to high atmospheric Hg. Conversely, the positive effect of wetland cover was dampened my proximity to power plants, suggesting that in landscapes with lower wetland coverage, atmospheric Hg concentrations determine organismal concentrations, yet that Hg concentrations of organisms within landscapes of high wetland coverage are determined by the greater methylation that occurs in these areas regardless of atmospheric Hg concentrations.

Unlike extrinsic factors in the environments *M. temminckii* occupies, body size of individuals did not correlate significantly with variation in THg concentrations. Although past studies have observed higher THg levels in larger turtles (Schneider et al. 2010, Hopkins et al. 2013b), lack of correlation between the two variables is widely observed in many turtle species. In many locations, body size is not predictive of THg concentrations in *C. serpentina* (Golet and Haines 2001, Helwig and Hora 1983, Hopkins et al. 2013b). Similarly, concentrations in six species of turtles of South America were uncorrelated with size (Schneider et al. 2010, Eggins et al. 2015). It is possible that the weak relationship results because turtles in many of these studies were sampled across multiple locations (e.g., Golet and Haines 2001, Schneider et al. 2010) where exposure rates may differ and lead site-specific effects to cover the influence of size (*sensu* Hannappel et al. 2021, MacCrimmon et al. 1983). Turnquist et al. (2011) and Hopkins et al. (2013b) demonstrated that effects of *C. serpentina* body size on THg were location-specific. The fact that a similar watershed-dependent pattern was not supported by this study may be due to limited per-watershed sample size.

Positive relationships between body size and THg concentrations have been documented in fishes, and may be attributable to the positive correlation between size and age, and the increased total exposure experienced by older individuals (Kannan et al. 1998). This process would reveal a stronger pattern in taxa that continue to grow throughout their lives (e.g., some fishes and turtles; Mommsen 2001, Congdon et al. 2013). Through this process, the lack of correlation observed in this study could result from a weak correlation between *M. temminckii* size and age. Individuals of the species exhibit wide variation in growth rates (Trauth et al. 2016, Rosenbaum et al. in press), and support this as a possibility.

Patterns between body size and THg (or lack thereof) across species may also depend upon ontogenetic dietary shifts. As is the case for some fishes, larger individuals have a propensity to consume prey from higher trophic levels, and therefore are more prone to bioaccumulation (Mathers and Johansen 2011). A negative relationship or no relationship may result for species that shift to consuming lower trophic levels or species that experience no dietary shifts with increased size. *Podocnemis sextuberculata* (six-tuberculed Amazon River turtle) exhibited lower THg concentrations at larger sizes, though potential dietary changes in the species that could explain this pattern are unknown (Schneider et al. 2009). Conversely, the catfish *Clarias gariepinus* is known to maintain a constant diet regardless of size, and in turn size classes do not vary significantly in THg concentration (Desta et al. 2007). *Macrochelys temminckii* exhibits a diverse diet (Elsey 2006), and the relative lack of correlation between size and THg concentrations observed in this study could arise from larger individuals feeding on lower trophic levels or across a wider array of sources. However, ontogenetic dietary changes in the species have not been quantified.

Chelydra serpentina also utilizes a wide breadth of food sources; therefore, the similarity in the average concentrations documented from this species (e.g., 0.05 – 0.3 ppm ww [Helwig and Hora 1983], 0.05 – 0.5 ppm ww [Golet and Haines 2001], 0.14 ppm dw [Lander et al. 2017]) and *M. temminckii* in this study were expected. In the Amazon River basin, podocnemids, which are predominantly herbivorous (Cunha et al. 2020), exhibit lower muscle concentrations (0.03 – 0.11 ppm ww) than chelydrids, while *Chelus fimbriata* (matamata), an obligately piscivorous turtle, has a higher average concentration (0.43 ppm; Schneider et al. (2010). These findings are consistent with occupants of higher trophic positions exhibiting greater THg loads.

However, in highly contaminated areas, *C. serpentina* accumulates high muscle THg concentrations (e.g., 15.6 ppm [Landler et al. 2017] and 32.3 ppm [Hopkins et al. 2013b]) that are negatively associated with fecundity and hatchling behavior. None of the *M. temminckii* sampled in eastern Texas exhibited levels seen from *C. serpentina* that inhabited directly contaminated water. However, assuming *M. temminckii* mercury accumulation results in deleterious effects at magnitudes similar to those observed in *C. serpentina*, populations exposed to waters contaminated with high levels of Hg, such as the Wigginsville Road Groundwater Plume Site (San Jacinto watershed, Montgomery County, Texas) (Texas Commission on Environmental Quality 2021), may be at risk of deleterious reproductive and developmental effects.

Regardless of toxicological effects that may manifest in turtles, there are health risks to humans who frequently consume *M. temminckii.* These risks are greatest to children and women of child-bearing age whose diets may expose their offspring *in utero* (Bose-O'Reilly et al. 2010). To curtail risk of dietary exposure, the United States Environmental Protection Agency (EPA) recommends limiting consumption of food with average THg concentrations between 0.23 and 0.46 ppm to one serving per week (U.S. EPA-FDA Fish Advice 2021). As of 2022, Mississippi and Louisiana were the only states in the native range of *M. temminckii* that allow its legal harvest. In Mississippi, take of one *M. temminckii* per year is permitted (Mississippi Department of Wildlife, Fisheries, and Parks 2022). Abiding by this regulation should keep consumers below the EPA-recommended limit, assuming average concentrations in Mississippi are similar to those observed in Texas. However, in Louisiana, one may legally harvest one turtle per day (Louisiana Department of Wildlife and Fisheries 2021), and given the concomitant potential for consumption every day, those who regularly supplement their diet within the harvest limits may be exposed to deleterious levels of THg. Illegal harvest for personal subsistence and purchases of *M. temminckii* meat from the black market (e.g., Eastern District of Texas 2017), as well as regular subsistence on other aquatic organisms (Chang et al. 2003) provide further opportunities for dietary exposure to THg above the consumption limit recommendations.

This study confirmed that *M. temminckii* accumulates high levels of THg according to watershed and habitat characteristics that likely influence biogeochemical cycling of the metal. Individual body size will not reasonably predict internal concentrations, indicating that variation in the species' Hg levels is dependent on extrinsic processes rather than intrinsic features of individuals. Future studies may benefit from exploring potential dietary shifts of the species in greater detail, which would lead to inference on the risks the species faces from dietary exposures to numerous contaminants. Furthermore, assessments of single populations exposed to uniform levels of THg may be able to elucidate potential effects of how size and age affect mercury levels in turtles.

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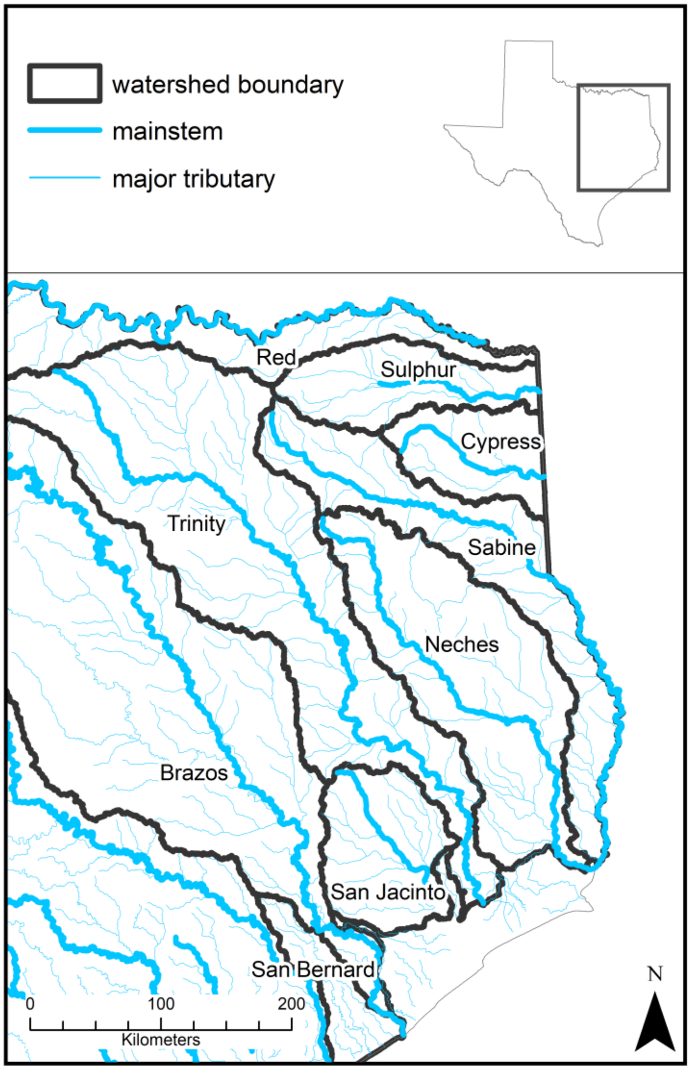
APPENDIX

Appendix 1. Watersheds, river mainstems, and major tributaries of the study area in eastern Texas, United States. The San Bernard, Brazos, San Jacinto, Trinity, Neches, and Sabine watersheds drain directly into the Gulf of Mexico. The Cypress and Sulphur Rivers in the northern portion of the survey area confluence with the Red River in Louisiana, and watersheds of all three of these rivers are part of the greater Mississippi watershed.



Appendix 2. Count histories of *Macrochelys temminckii* for surveys (*y*) at 48 sites used in occupancy and abundance models. Integers listed after "+" indicate number of recaptures during respective surveys, which were not used in multinomial *N*-mixture models. To protect locations of species occurrence, sites are identified by their respective counties. NA denotes that a survey did not occur.

Site ID	y_1	y_2	y_3	**Site ID**	y_1	y_2	y_3
Anderson Co.	11	1+1	5	Lamar Co. #1	0	0	0
Angelina Co.	4	1	4	Lamar Co. #2	0	0	NA
Bowie Co.	0	0	0	Leon Co.	11	1+2	1
Brazoria Co. #1	0	0	0	Liberty Co.	0	0	0
Brazoria Co. #2	0	0	0	Nacogdoches Co #2	0	0	1
Brazos Co.	0	0	0	Nacogdoches Co. #1	6	0	1+1
Camp Co. #1	0	0	0	Navarro Co. #1	0	0	0
Camp Co. #2	1	1	0	Navarro Co. #2	4	5	1+1
Cass Co.	1	0	2	Red River Co.	0	0	0
Chambers Co.	7	3	1+1	Rockwall Co. #1	0	0	0
Cherokee Co.	7	5+1	3+1	Rockwall Co. #2	0	NA	NA
Collin Co.	0	1	0	San Augustine Co.	0	0	2
Delta Co.	0	0	0	San Jacinto Co.	1	1	1
Ellis Co.	0	0	0	Shelby Co.	3	0	1
Fannin Co.	0	0	0	Titus Co.	0	1	0
Fort Bend Co.	0	0	0	Trinity Co.	2	4	1
Grayson Co.	0	0	0	Tyler Co.	7	2+3	2
Grimes Co.	0	0	0	Upshur Co.	2	0	0
Harrison Co. #1	4	2	1	Van Zandt Co.	1	2	0
Harrison Co. #2	1	2	2	Walker Co.	1	0	1
Houston Co.	6	8+1	2	Waller Co. #1	7	0	2+1
Hunt Co.	7	3	6	Waller Co. #2	0	NA	NA
Jasper Co.	3	1	1	Wood Co. #1	1	1	1+1
Kaufman Co.	0	0	1	Wood Co. #2	8	2+1	2+1

Appendix 3. Complete list of models considered for determining occurrence and counts of *M. temminckii* across three spatial scales. Bolded models are within a cumulative weight of 0.95 (i.e., 95% confidence model set *sensu* Symonds and Moussalli 2011). By convention, *r* is used to represent individual detection probability for Royle-Nichols models.

Detection covariate-only models

Static site occupancy model		Model	K	AICc	ΔAICc	w_i	LL
global GOF		**_p_(flow + lunar + lunar^2 + NND) Ψ(.)**	6	143.28	0.00	0.59	-64.62
P	ĉ	**_p_(flow + lunar + lunar^2 + NND + date + temp) Ψ(.)**	8	144.52	1.24	0.32	-62.42
0.304	1.15	**_p_(flow + temp) Ψ(.)**	4	149.50	6.22	0.03	-70.29
		_p_(flow + NND) Ψ(.)	4	149.58	6.30	0.03	-70.33
		p(flow + lunar + lunar^2) Ψ(.)	5	150.08	6.80	0.02	-69.33
		p(flow) Ψ(.)	3	151.74	8.46	0.01	-72.60
		p(lunar + lunar^2) Ψ(.)	4	152.94	9.66	0.00	-72.01
		p(.) Ψ(.)	2	158.08	14.79	0.00	-76.90
		p(NND) Ψ(.)	3	158.50	15.22	0.00	-75.98
		p(date) Ψ(.)	3	159.67	16.39	0.00	-76.56
		p(temp) Ψ(.)	3	160.31	17.03	0.00	-76.88
Royle-Nichols *N*-mixture model							
global GOF		**_r_(flow + lunar + lunar^2+ NND) λ(.)**	6	140.51	0.00	0.70	-63.23
P	ĉ	**_r_(flow + lunar + lunar^2 + NND + date + temp) λ(.)**	8	142.91	2.39	0.21	-61.61
0.282	1.2	**_r_(flow + NND) λ(.)**	4	146.39	5.88	0.04	-68.73
		_r_(flow + temp) λ(.)	4	147.45	6.93	0.02	-69.26
		r(flow + lunar + lunar^2) λ(.)	5	148.24	7.72	0.01	-68.40
		r(flow) λ(.)	3	149.17	8.66	0.01	-71.31
		r(lunar + lunar^2) λ(.)	4	150.93	10.42	0.00	-71.00
		r(NND) λ(.)	3	155.06	14.54	0.00	-74.26
		r(.) λ(.)	2	155.78	15.27	0.00	-75.76
		r(date) λ(.)	3	157.51	16.99	0.00	-75.48
		r(temp) λ(.)	3	158.02	17.50	0.00	-75.74
Multinomial *N*-mixture model							
global GOF		**_p_(flow + NND) λ(.)**	5	51.90	0.00	0.69	-20.23
P	ĉ	**_p_(flow + lunar + lunar^2 + NND) λ(.)**	7	53.96	2.06	0.24	-18.58
0.393	1.02	**_p_(NND) λ(.)**	4	57.30	5.40	0.05	-24.18
		p(flow + date + date^2 + NND + lunar + lunar^2) λ (.)	9	59.73	7.84	0.01	-18.50

(continued)

		p(flow + lunar + lunar^2) λ(.)	4	61.76	9.86	0.00	-26.42
		p(flow + date + date^2) λ(.)	5	64.16	12.27	0.00	-26.37
		p(flow + lunar + lunar^2) λ(.)	6	65.21	13.32	0.00	-25.58
		p(.) λ(.)	3	65.60	13.70	0.00	-29.53
		p(lunar + lunar^2) λ(.)	5	67.82	15.92	0.00	-28.20
		p(date) λ(.)	4	67.95	16.05	0.00	-29.51
		p(flow + lunar + lunar^2 + date) λ(.)	8	69.05	17.15	0.00	-24.68
		p(date + date^2) λ(.)	5	70.45	18.55	0.00	-29.51
		Subwatershed covariate state process models					
Static site occupancy model		Model	K	AICc	ΔAICc	w_i	LL
global GOF		**Ψ(forest)**	7	132.88	0.00	0.54	-58.04
P	ĉ	**Ψ(forest + developed)**	8	135.65	2.77	0.14	-57.98
0.488	0.86	**Ψ(forest + wetland)**	8	135.66	2.78	0.14	-57.98
		Ψ(forest + open)	8	135.77	2.89	0.13	-58.04
		Ψ(forest + open + wetland)	9	138.67	5.79	0.03	-57.97
		Ψ(developed + open)	8	141.33	8.46	0.01	-60.82
		Ψ(forest + developed + open + wetland)	10	141.82	8.94	0.01	-57.93
		Ψ(open)	7	142.69	9.81	0.00	-62.95
		Ψ(developed)	7	143.25	10.37	0.00	-63.23
		Ψ(.)	6	143.28	10.40	0.00	-64.62
		Ψ(wetland)	7	143.56	10.68	0.00	-63.38
Royle-Nichols *N*-mixture model							
global GOF		**λ(forest)**	7	134.90	0.00	0.29	-59.05
P	ĉ	**λ(forest + wetland)**	8	135.45	0.56	0.22	-57.88
0.548	0.79	**λ(developed + forest)**	8	136.44	1.55	0.13	-58.38
		λ(crops + forest + wetland)	9	136.77	1.87	0.11	-57.01
		λ(forest + open)	8	137.79	2.89	0.07	-59.05
		λ(developed + open)	8	138.10	3.20	0.06	-59.20
		λ(developed)	7	138.87	3.98	0.04	-61.04
		λ(forest +developed + open + wetland)	10	139.97	5.07	0.02	-57.01
		λ(.)	6	140.51	5.62	0.02	-63.23
		λ(open)	7	140.59	5.70	0.02	-61.90
		λ(wetland)	7	140.95	6.06	0.01	-62.08
Multinomial *N*-mixture model							
global GOF		**λ(.)**	5	51.90	0.00	0.33	-20.23
P	ĉ	**λ(forest)**	6	53.31	1.41	0.16	-19.63

(continued)

0.323	1.07	**λ(developed)**	6	54.02	2.12	0.11	-19.99
		λ(wetland)	6	54.34	2.44	0.10	-20.14
		λ(open)	6	54.39	2.49	0.10	-20.17
		λ(forest + open)	7	55.79	3.89	0.05	-19.50
		λ(developed + forest)	7	55.80	3.91	0.05	-19.50
		λ(forest + wetland)	7	55.86	3.96	0.05	-19.53
		λ(developed + open)	7	56.64	4.74	0.03	-19.92
		λ(open + forest + wetland)	8	57.24	5.34	0.02	-18.78
		λ(developed + forest + open + wetland)	9	60.21	8.31	0.01	-18.74
		Geographic location covariate state process models					
Static site occupancy model		Model	K	AICc	ΔAICc	w_i	LL
global GOF		**Ψ(latitude + latitude^2 + longitude)**	9	129.78	0.00	0.99	-53.52
P	ĉ	Ψ(.)	6	143.28	13.50	0.00	-64.62
0.292	1.19	Ψ(latitude + longitude)	6	147.72	17.64	0.00	-66.83
Royle-Nichols *N*-mixture model							
global GOF		**λ(latitude + latitude^2 + longitude)**	9	133.52	0.00	0.96	-55.39
P	ĉ	λ(.)	6	140.51	6.99	0.03	-63.23
0.504	0.82	λ(latitude + longitude)	8	143.31	9.79	0.01	-61.81
Multinomial *N*-mixture model							
global GOF		**λ(latitude + latitude^2 + longitude)**	8	47.14	0.00	0.91	-13.73
P	ĉ	**λ(.)**	5	51.90	4.75	0.08	-20.23
0.245	1.14	λ(latitude + longitude)	7	56.50	9.35	0.01	-19.85
		Local habitat covariate state process models					
Static site occupancy model		**Model**	K	AICc	ΔAICc	*wi*	LL
global GOF		**Ψ(.)**	6	143.28	0	0.49	-64.62
P	ĉ	**Ψ(canopy + debris)**	8	144.36	1.08	0.28	-62.33
0.292	1.29	**Ψ(debris + float. veg)**	8	145.90	2.62	0.13	-63.11
		Ψ(canopy + debris + veg + HAI + sinuosity)	9	146.81	3.53	0.08	-62.04
		Ψ(HAI)	5	151.63	8.35	0.01	-70.10
		Ψ(sinuosity)	5	151.88	8.59	0.01	-70.22
Royle-Nichols *N*-mixture model							
global GOF		**λ(.)**	6	140.51	0	0.45	-63.23
P	ĉ	**λ(HAI)**	7	142.34	1.83	0.18	-62.77
0.45	0.99	**λ(sinuosity + depth)**	8	142.83	2.32	0.14	-61.57
		λ(sinuosity)	7	143.24	2.73	0.12	-63.22
		λ(debris + veg)	8	143.95	3.43	0.08	-62.13

(continued)

		λ(canopy + debris)	9	146.04	5.53	0.03	-61.65
		λ(canopy + debris + veg + HAI + sinuosity)	12	152.35	11.84	0.00	-59.72
Multinomial *N*-mixture model							
global GOF		**λ(.)**	5	51.9	0	0.54	-20.23
P	$\hat{c}$	**λ(sinuosity)**	6	54.31	2.41	0.16	-20.13
0.245	1.14	**λ(HAI)**	6	54.49	2.59	0.15	-20.22
		λ(canopy + debris)	7	56.4	4.5	0.06	-19.80
		λ(sinuosity + depth)	7	56.71	4.81	0.05	-19.96
		λ(debris + float. veg.)	7	57.02	5.12	0.04	-20.11
		λ(canopy + debris + veg + HAI + sinuosity)	11	67.33	15.43	0.00	-19.00

Appendix 4. Comparison of *Macrochelys temminckii* catch per unit effort (CPUE) with expected abundance ($\hat{\lambda}_i$) calculated from the top-ranked multinomial *N*-mixture model, as well as with empirical Bayes' count estimates conditional on the observed data and estimates of $\hat{\lambda}_i$ and p ($\hat{N}_i$). Widest CIs occurred at locations at middle latitudes and extremes of longitude within the study region. Horizontal lines organize sites by watershed ordered from southwest to northeast (San Bernard, Brazos, San Jacinto, Trinity, Neches, Sabine, and Mississippi watersheds).

Site	**CPUE**	$\hat{N}_i$	$\hat{N}_i$ **95% CI**	$\hat{\lambda}_i$	$\hat{\lambda}_i$ **95% CI**
Brazoria Co. #1	0	0.612	0 - 3	0.864	0.167 - 4.457
Brazos Co.	0	8.167	0 - 31	9.250	3.675 - 23.280
Waller Co. #2	0	3.030	0 - 12	4.837	1.954 - 11.974
Grimes Co.	0	1.728	0 - 8	9.175	4.168 - 20.197
Brazoria Co. #2	0	0.369	0 - 2	0.947	0.198 - 4.531
Fort Bend Co.	0	0.408	0 - 2	2.853	1.001 - 8.133
San Jacinto Co.	0.067	3.642	3 - 6	8.093	4.496 - 14.567
Waller Co. #1	0.237	17.047	11 - 26	5.083	2.227 - 11.602
Walker Co.	0.044	2.327	2 - 4	8.995	4.779 - 16.933
Navarro Co. #1	0	5.143	0 - 20	10.682	4.974 - 22.942
Anderson Co.	0.378	18.818	17 - 22	12.063	6.384 - 22.791
Leon Co.	0.289	15.849	13 - 20	13.471	7.061 - 25.699
Kaufman Co.	0.022	1.596	1 - 4	7.511	3.647 - 15.470
Rockwall Co. #1	0	4.242	0 - 17	4.357	1.946 - 9.758
Liberty Co.	0	0.522	0 - 3	4.081	1.792 - 9.294
Navarro Co. #2	0.222	16.258	11 - 23	11.599	5.088 - 26.442
Collin Co.	0.022	1.947	1 - 5	3.764	1.640 - 8.639
Chambers Co.	0.244	13.280	11 - 17	3.581	1.469 - 8.729
Ellis Co.	0	2.176	0 - 9	9.130	3.779 - 22.057
Nacogdoches Co. #2	0.022	12.607	2 - 35	13.827	7.626 - 5.071
San Augustine Co.	0.044	3.468	2 - 7	13.824	6.403 - 29.850
Trinity Co.	0.178	8.231	7 - 11	13.602	7.617 - 24.291
Tyler Co.	0.244	13.066	11 - 17	10.078	4.785 - 21.229
Nacogdoches Co. #1	0.231	7.474	7 - 9	13.833	7.587 - 25.220
Cherokee Co.	0.333	21.599	17 - 28	12.472	7.127 - 21.824
Jasper Co.	0.111	6.265	5 - 9	11.839	5.778 - 24.257
Van Zandt Co.	0.067	3.429	3 - 5	8.002	4.730 - 13.539
Angelina Co.	0.200	12.378	9 - 17	13.732	7.688 - 24.525

(continued)

Houston Co.	0.356	23.450	18 - 31	13.674	7.757 - 24.106
Wood Co. #2	0.267	12.881	2 - 15	7.131	4.305 - 11.811
Hunt Co.	0.356	28.409	21 - 39	3.783	1.896 - 7.548
Wood Co. #1	0.067	5.062	3 - 9	4.398	2.467 - 7.841
Rockwall Co. #2	0	0.699	0 - 4	4.386	2.069 - 9.299
Shelby Co.	0.089	4.456	4 - 6	12.695	5.504 - 29.280
Bowie Co.	0	1.313	0 - 6	2.479	1.042 - 5.902
Fannin Co.	0	0.510	0 - 3	0.914	0.275 - 3.040
Harrison Co. #1	0.156	13.360	8 - 21	6.404	2.909 - 14.094
Camp Co. #1	0	0.112	0 - 1	4.311	2.277 - 8.164
Red River Co.	0	0.037	0 - 1	0.776	0.217 - 2.769
Harrison Co. #2	0.111	5.807	5 - 8	6.689	3.066 - 14.592
Delta Co.	0	0.551	0 - 3	2.257	1.009 - 5.050
Grayson Co.	0	0.254	0 - 2	0.932	0.243 - 3.569
Upshur Co.	0.044	2.362	2 - 4	5.951	3.382 - 10.471
Lamar Co. #1	0	0.609	0 - 3	0.819	0.239 - 2.800
Camp Co. #2	0.044	2.299	2 - 4	4.532	2.409 - 8.526
Lamar Co. #2	0	0.094	0 - 1	0.975	0.310 - 3.069
Cass Co.	0.067	6.168	3 - 12	2.605	1.098 - 6.181
Titus Co.	0.022	1.720	1 - 4	2.419	1.074 - 5.449

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PUBLICATIONS

Rosenbaum, D., D.C. Rudolph, D. Saenz, L.A. Fitzgerald, R.E. Nelson, C.S. Collins, T.J. Hibbits, R.W. Maxey, P. Crump, C.M. Schalk. Distribution and demography of the alligator snapping turtle (*Macrochelys temminckii*) in Texas: a 20-year perspective. *In press*. Southeastern Naturalist.

Schalk, C.M., R.L. Antoniazzi, **D. Rosenbaum**, J.M. Arnett, A. Pelletier, C.S. Adams, W. Baxter-Bray. 2021. *Amphiuma tridactylum* (Three-toed Amphiuma) Geographic Distribution. Herpetological Review. 52:789.

CONFERENCE ACTIVITY/PARTICIPATION

2022. **Rosenbaum, D.**, D. Saenz, C.M. Schalk. Occupancy and abundance of the alligator snapping turtle (*Macrochelys temminckii*) in Texas. Ecological Integration Symposium, College Station, TX. Talk.

2022. **Rosenbaum, D.**, D. Saenz, C.M. Schalk. Distribution and occupancy of the alligator snapping turtle (*Macrochelys temminckii*) in Texas. Texas Chapter of the Wildlife Society Annual Meeting. Conference. Marble Falls, TX. 2nd Place Clarence Cottam Award. Talk

2022. **Rosenbaum, D.**, D. Saenz, C.M. Schalk. Mercury contamination in alligator snapping turtles (*Macrochelys temminckii*) of Texas. Texas Chapter of the Wildlife Society Annual Meeting. Conference. Marble Falls, TX. 1st place best graduate research Poster.

2021. T. Brownjohn, **D. Rosenbaum**, C.M. Schalk. Body condition and relative abundance of four turtle species across a gradient of ecological integrity. Arthur Temple College of Forestry and Agriculture Undergraduate Research Conference, Nacogdoches, TX. Poster.

2021. **Rosenbaum, D.**, D. Saenz, C.M. Schalk. Historical and contemporary results from alligator snapping turtle (*Macrochelys temminckii*) surveys in Texas. Southeast Partners in Amphibian and Reptile Conservation. Virtual Conference. Talk.

2021. **Rosenbaum, D.**, D. Saenz, C.M. Schalk. Historical and contemporary results from alligator snapping turtle (*Macrochelys temminckii*) surveys in Texas. Stephen F. Austin State University Graduate Research Conference. Virtual Conference. Talk.