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Detection, occupancy, and abundance of the alligator snapping turtle in Texas

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Abstract

The alligator snapping turtle (*Macrochelys temminckii*) is a long-lived species that is widely distributed across the southeastern United States. Both these characteristics make monitoring its occupancy and abundance particularly challenging. In 2020 and 2021, we conducted hoop trap surveys at 51 permanent water bodies across the Texas, USA, range of the species to estimate occupancy and average abundance with site occupancy models and multinomial *N*-mixture models, respectively. We confirmed the species to be present at 61% of surveyed locations. Mean detection probability was 0.77, and was influenced methodologically by the spacing of traps, and environmentally by lunar phase and water flow velocity. Mean occupancy probability was 0.82, and mean estimated abundance was 7.57 turtles/site. Our data provided evidence that the species has a higher occurrence probability in waters of highly forested catchments, and is most probable to occur in highest abundances at median latitudes within its Texas range. Despite known microhabitat preferences of the species, instream habitat characteristics (e.g., canopy coverage, depth, sinuosity) did not strongly influence its occupancy or abundance. Spatial dynamics of the occupancy and abundance of the species in Texas are influenced by landscape features more than local habitat. These results further corroborate the importance of watershed land cover to aquatic organisms, and our methods provide a standardized template for monitoring and quantifying important demographic parameters

of the species across multiple locations while accounting for imperfect detection.

KEYWORDS

aquatic ecology, forest cover, long-lived organism, *Macrochelys temminckii*, occurrence, range edge, removal sampling, turtle

Freshwater ecosystems are experiencing habitat alteration and species declines worldwide (Wohl 2019). Direct anthropogenic modifications may alter flood pulses, temperature, flow rate, and increase siltation and microhabitat homogenization (Benke 1990, Magilligan and Nislow 2005, Riedle et al. 2005, Wohl 2019). 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 alteration (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, Webb et al. 2002, Howey and Dinkelacker 2013). These traits cause reliance on high adult survivorship for population persistence, which increases susceptibility to overexploitation and extirpation (Reed et al. 2002).

Understanding spatial and temporal trends in occurrence and abundance is integral to monitoring populations of such organisms that are susceptible to declines (Kéry and Schmidt 2008). 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). In monitoring efforts, such apparent patterns in abundance are confounded by detection probability (p), as the 2 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; Lawton 1993, Doherty et al. 2003, Royle and Nichols 2003). Detectability may also be dependent on other factors, including environmental characteristics (Durso et al. 2011, Price 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).

Environmental and anthropogenic effects on aquatic turtles are often inferred from hoop trap surveys (Hollender and Ligon 2021, Mota et al. 2021, Ostovar et al. 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). The 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 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 et al. 1996, Rudolph et al. 2002), over a variety of environmental conditions and habitat characteristics (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 (Morreale et al. 1984). There are always uncontrollable factors in field settings, which may limit the use of CPUE as a useful 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 trapping has use beyond that of a nuisance parameter; it may also provide valuable insight on turtle ecology. As a result, some aquatic turtle studies have

accounted for and modeled *p* (Sterrett et al. 2010, Stokeld et al. 2014, Dreslik et al. 2017, Buchanan et al. 2019, Johnson 2020), 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 alligator snapping turtle (*Macrochelys temminckii*) (Jensen and Birkhead 2003, Riedle et al. 2005, Boundy and Kennedy 2006, Howey and Dinkelacker 2013, Huntzinger et al. 2019). Many studies using these surveys assume CPUE to be an adequate proxy of relative abundance (Folt and Godwin 2013, Lescher et al. 2013, King et al. 2016, Huntzinger et al. 2019). With a few exceptions (Dreslik et al. 2017, Johnson 2020), hoop trap surveys do not explicitly account for environmentally caused variation in *p*. As potential sources of such variation, there is evidence alligator snapping turtles may decrease activity and be captured at lower rates during temperature extremes brought about during summer and winter (Riedle et al. 2006, Fitzgerald and Nelson 2011, Munscher et al. 2020), and Pritchard (2006) reported an anecdote that capture rate of the species decreased during bright, full moon nights. Nevertheless, CPUE is the only index currently available for inference on the relative abundance and distribution of the alligator snapping turtle across its range.

Habitat alteration and harvest are primary threats to the persistence of the alligator snapping turtle (Riedle et al. 2005). Consequently, states where it occurs have implemented protective regulations or, at minimum, recreational harvest limits (Reed et al. 2002, Louisiana Fisheries 2004). The United States Fish and Wildlife Service has considered listing the species under the Endangered Species Act since 1982 (Environmental Conservation Online System 2021), and in 2021 proposed threatened status after completing a species status assessment. Prior surveys and historical distribution records indicate that the distribution of the alligator snapping turtle is contracting from its northern and western edges (e.g., OK, IL, KY; Riedle et al. 2008*a*, Bluett et al. 2011, Baxley et al. 2014). Because of this range contraction, populations in Texas, USA, are important to examine in detail, as they occur along the southwestern range edge of the species. In Texas, the populations of the species occur within watersheds that drain into the Gulf of Mexico from the San Jacinto and Trinity rivers eastward, and tributaries of the Mississippi watershed (Dixon 2013, Hibbitts and Hibbitts 2016, Munscher et al. 2021, Rosenbaum et al. 2023).

Within its range, the alligator snapping turtle may occur 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). In these waters, it exhibits specific microhabitat preferences (Harrel et al. 1996*a*, 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 (*Castor canadensis*) dams, submerged trees and overhanging vegetation (Riedle et al. 2006, Howey and Dinkelacker 2009, Moore et al. 2014).

Our objective was to survey alligator snapping turtles across the purported range of the species in Texas to gain insight on landscape (i.e., watershed) and local habitat variables that influence and predict its distribution and patterns of abundance. We predicted a decrease in *p* during summer when water temperatures are relatively high. Because the species' morphology is conducive to greater hydrodynamic drag relative to other turtles and well adapted to benthic habits, we posited that increased flow velocity would further decrease *p*. We 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 corroborated an anecdote of low alligator snapping turtle capture rate on bright nights (Pritchard 2006). In regard to trapping efficacy, we predicted that density of traps would positively influence *p*. In regard to occurrence, we 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, we hypothesized that increased proportions of wetland cover and forest, indicators of alligator snapping turtle habitat availability, would increase occupancy probability and abundance,

while greater developed and agricultural watershed cover would show the opposite relationship by reducing habitat suitability.

STUDY AREA

We conducted this study during April to October 2020 and March to August 2021 across the putative geographic range of the alligator snapping turtle in eastern Texas within the Red, Cypress, Sulphur, Sabine, Neches, Trinity, San Jacinto, Brazos, and San Bernard river watersheds (Figure 1). The northern and eastern extent of the study area was characterized by pine (*Pinus* spp.) forest in upland areas. In the southern extent of the area, which consisted of coastal plain, upland vegetation communities transitioned to grassland, whereas the western portion of the area was characterized by arid Post Oak (*Quercus stellata*) Savanna and Blackland Prairie ecoregions (Griffith et al. 2007). Floodplains throughout the area were dominated by deciduous forest (Griffith et al. 2007). The most frequent tree taxa we documented within sampling sites were water elm (*Planera aquatica*), bald cypress (*Taxodium distichum*), green ash (*Fraxinus pennsylvanica*), oak (*Quercus* spp.), boxelder

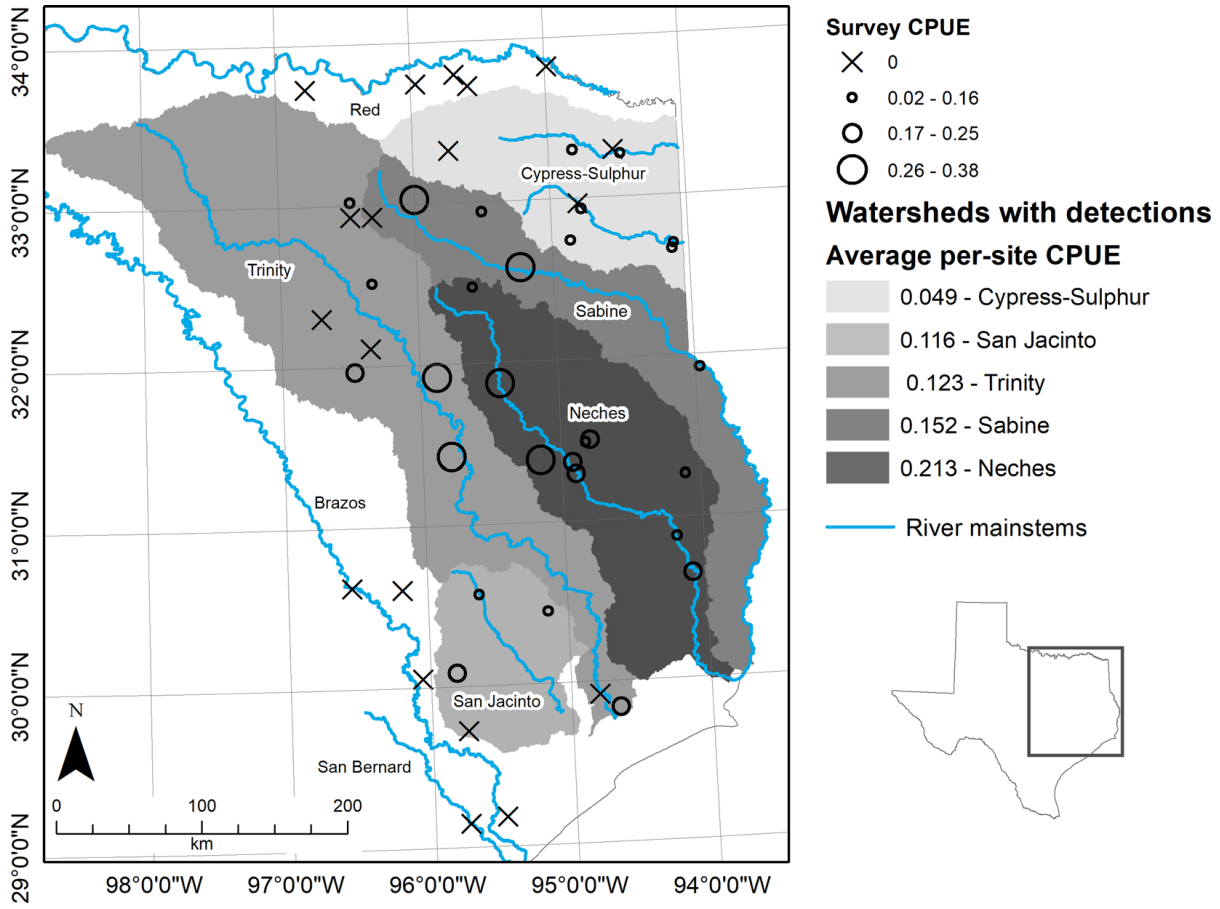

FIGURE 1 Site locations depicting variation in catch per unit effort (CPUE) of the alligator snapping turtle sampled from May 2020 to August 2021 in eastern Texas, USA. Catch per unit effort averages of the Cypress and Sulphur watersheds are calculated separately from sites in the Red River mainstem watershed, where no individuals were detected. River mainstems of the study area are depicted in blue. The Cypress and Sulphur rivers in the northern portion of the survey area confluence with the Red River in Louisiana, USA, and watersheds of all 3 of these rivers are part of the greater Mississippi watershed.

(*Acer negundo*), black birch (*Betula nigra*), American elm (*Ulmus americana*), and willow (*Salix* spp.). Major land use throughout the area included silviculture, agriculture, and urban development (Griffith et al. 2007), the latter of which was most prominent in the northern Blackland Prairie around the Dallas Fort Worth Metroplex and in the coastal plain surrounding Houston.

Potential predators of the alligator snapping turtle or its nests that occurred in the area include, but are not limited to, the river otter (*Lontra canadensis*), American alligator (*Alligator mississippiensis*), racoon (*Procyon lotor*), and the nine-banded armadillo (*Dasypus novemcinctus*; Ligon and Reasor 2007, Holcomb and Carr 2013). Aquatic vertebrate communities in the area consisted of various fish, turtle, snake, and amphibian species. We documented the razor-backed musk turtle (*Sternotherus carinatus*), spiny softshell (*Apalone spinifera*), pond slider (*Trachemys scripta elegans*), common snapping turtle (*Chelydra serpentina*), and false map turtle (*Graptemys pseudogeographica kohni*) in syntopy with the alligator snapping turtle.

In the area, mean annual precipitation increased along an eastward gradient, and ranged from 94 cm to 139 cm from 1970 to 2000 at surveyed sites (Fick and Hijmans 2017). The climate was humid subtropical (Kottek et al. 2006), and mean annual winter temperatures generally decreased to the north. Winter weather generally occurred November through March, and warmest summer temperatures occurred June through August. Mean January temperatures ranged from −1°C in the northern Blackland Prairie to 17°C on the coastal plain, whereas mean July temperatures of the study area ranged from 22°C to 34°C (Griffith et al. 2007). Elevation of sampling sites ranged from approximately 9 m above sea level in the coastal plain to 183 m above sea level at the northwestern portion of the study area.

Within the study area, we surveyed reservoirs, oxbows, sloughs, river mainstems, and tributaries. In a previous survey of the species' distribution in Texas (Rudolph et al. 2002), 21 sites throughout watersheds of its known range and 2 additional sites beyond its known range within the Brazos watershed were surveyed (Rudolph et al. 2002, Rosenbaum et al. 2023). We resurveyed 22 of these 23 sites and an additional 29 sites in counties that the alligator snapping turtle is suspected or known to inhabit (n = 51 sites; Rosenbaum et al. 2023). The region encompassed by these sites spanned approximately 110,000 km^2.

METHODS

Site selection

In the previous study (Rudolph et al. 2002), sites were purposively selected to represent every Texas river drainage the alligator snapping turtle is known or suspected to occur (Figure 1; C. S. Collins, SWCA Environmental Consultants, personal communication). Additional purposively selected survey sites were limited to a specific set of counties to help fill knowledge gaps of the Texas distribution of the species (Rosenbaum et al. 2023). We used 3 criteria to determine if aquatic habitats in these locations were suitable for trapping: accessibility via public access points or landowner permission (Sweeten and Ford 2016), navigability by foot or boat, and no habitat constraints (i.e., limited channel depth and width) that would prevent submergence of trap funnels. We sampled only sites that were permanent and exhibited at least ephemeral connection with tributaries because of the predominantly aquatic habits and poor overland dispersal ability of the species.

Because of this nonrandom 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, selected sites have the potential to become reference monitoring sites for the species.

Field surveys

We used single-funnel, finger-throated, 4-hoop traps (hoop diameter = 1.2 m; mesh size = 2.54 cm) baited with fish to detect alligator snapping turtles. We predominantly used cuts of common carp (*Cyprinus carpio*) as bait, but we used buffalo (*Ictiobus* spp.), temperate bass (*Morone* spp.), freshwater drum (*Aplodinotus grunniens*), and catfish (*Ictalurus* spp.) occasionally to supplement common carp. We suspended fish from the rear hoop of each trap in a holding canister. Each canister was constructed of 7.6-cm × 30.5-cm polyvinyl chloride 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 ≥1 turtles entered a trap.

We standardized site visits to 3 consecutive surveys per site, with 15 baited hoop traps deployed per survey. Therefore, we allocated 45 trap-nights of survey effort to most sites. During 8 site visits, logistical constraints such as flood events and trap theft resulted in fewer surveys and fewer hoop traps per survey (Appendix A). We surveyed 2 sites only 2 times, and 1 site only 1 time.

Each of the 3 surveys at a site began when we baited and deployed traps. In lotic waters, we deployed traps upstream of aquatic structures, undercuts, or low energy pools, when present. In lentic systems, we 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 105 m. We left traps in place overnight (~24 hr) and then checked for captures, which concluded the survey. We measured, sexed, and marked all captured alligator snapping turtles before their release (Nagle et al. 2017). We then replaced bait prior to re-deploying traps, at which point a subsequent survey began. We used fresh bait for each survey because alligator snapping turtle 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. We determined per-site CPUE as the number of individual alligator snapping turtles captured divided by the number of trap-nights across all surveys. We did not include recapture events in the calculation (Boundy and Kennedy 2006, Lescher et al. 2013).

Habitat variables

We recorded the presence or absence of floating vegetation, submerged and emergent vegetation, and woody debris within a 5-m radius of each trap, and measured canopy cover above each trap opening with a spherical densiometer (Strickler 1959). We also recorded maximum water depth at trap opening, wetted channel width, and decimal degree coordinates (to 6 decimal places; World Geodetic System 1984 datum) at each trap. We included habitat variables collected at each trap in site-scale analyses of occupancy and abundance by averaging measures within each site (Perinchery et al. 2011).

Many sitewide variables were related to anthropogenic influence and human accessibility. These included the number of passive fishing lines (i.e., trotlines [limblines, juglines]) observed and 16 binary categorical variables (Table 1). We compiled these into an additive index to serve as a covariate of occupancy and abundance that approximated human accessibility (i.e., 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. Therefore, their numbers accumulate in frequently fished areas, and provide insight on long-term fishing pressure. Not all trotlines were detected in sites because of observation error, so numbers are underestimated. To account for uncertainty in counts, we assigned the numbers observed to 1 of 3 ordinal categories, each of which corresponded with an additive value for the index (Table 1). Other site variables included surface water temperature (°C) and flow velocity (m/sec). We used latitude and longitude (decimal degree

TABLE 1 Factors used to quantify human accessibility index values of each site sampled for alligator snapping turtles in eastern Texas, USA, May 2020–August 2021.

Factor	Points to index
Presence of footpaths to (but not along) waterbody	1
Presence of footpaths also running along waterbody	1
Presence of fishing docks	1
Presence of other structures (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

coordinates; World Geodetic System 1984 datum) of site access points as site covariates of occupancy and abundance after we documented a strong unimodal latitudinal gradient in CPUE across the watersheds surveyed (Rosenbaum et al. 2023).

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

We 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 of 1983. We obtained land cover type data from the conterminous United States National Land Cover Database (NLCD) updated in 2019 (NLCD 2019, Dewitz and U.S. Geological Survey [USGS] 2021). From the 16 cover categories into which this dataset organizes land of the United States, we developed 4 broad cover categories for analysis: 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 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 the

alligator snapping turtle. For example, the species occurs in woody wetlands and herbaceous wetlands dominated by plants such as buttonbush (*Cephalanthus* spp.) or cattail (*Typha* spp.; Harrel et al. 1996*a*). Furthermore, compiling similar cover types into 1 reduces the number of parameters to model.

We delimited sites by subwatershed (12-digit hydrologic unit) polygons provided by the Watershed Boundary Dataset of USGS (USGS 2020). These boundaries are delineated by topography and surface water flow, so they define biologically relevant units of the landscape (USGS 2009). For cases in which >1 site occurred in the same subwatershed polygon, we considered only the first site surveyed for further analysis to prevent repeat values. This resulted in 48 samples out of the 51 sites surveyed. We then calculated the proportions of the 4 land cover types in each subwatershed. We used the national hydrography dataset flowline polylines limited to the farthest upstream trap and farthest downstream trap of each site to calculate site waterbody lengths (USGS 2020). We standardized these values to the linear distance between the traps to quantify sinuosity. In lotic sites, we calculated surface area as the average wetted channel width multiplied by national hydrography dataset flowline polylines used in sinuosity calculation. In lentic sites, we calculated area as the minimum convex polygon connecting trap coordinates, excluding sections encompassing land. We used these values to estimate average alligator snapping turtle density from the average abundance estimate.

Data analysis

Detection and count data obtained by field sampling enabled analysis of both occupancy and abundance of the species and the environmental variables that influence p. Modeling occupancy and abundance together enabled us to ascertain the degree to which detection and nondetection data are sufficient to approximate abundance (Linden et al. 2017), and the extent to which local density of turtles may influence detection probability (Tanadini and Schmidt 2011). We analyzed survey data using hierarchical models each consisting of 2 submodels. One submodel describes false-negative error rates in observation data (species detection and 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_i) and site population size (N_i) during surveys were the latent variables considered. In the context of ecological studies, the false-negative error rate describes p.

We z-standardized all continuous covariate values used to model occupancy probability and abundance (Taillie et al. 2015, Kéry and Royle 2016). Prior to fitting models, we calculated Pearson's correlation coefficients (r) for each pair of covariates. For pairs of covariates with $r > 0.6$, we considered only 1 of the pair for modeling to minimize collinearity.

We analyzed models using frequentist inference and maximum likelihood estimation of parameters. We inferred relative model fit with an information-theoretic perspective using likelihood, Akaike's Information Criterion corrected for sample size (AIC_c), and Akaike weights (w_i; Burnham and Anderson 2002). To determine which covariates best predicted occupancy and abundance, we adopted a sequential-by-sub-model selection strategy (Morin et al. 2020), in which we 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, we independently ranked 3 suites of models categorized by covariates pertaining to geographic location, subwatershed land cover, or local habitat characteristics (Table 2). After fitting global models for each of these suites, we calculated the variance inflation factor of each covariate in the global model. If the variance inflation factor of a covariate was >5, we dropped it from analysis to minimize multicollinearity. We fitted all models using the R package unmarked (Fiske and Chandler 2011). We computed model selection 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 and nondetection data to estimate p of the considered species, conditional on

TABLE 2 Descriptions and labels of covariates used to model detection, occupancy, and abundance of the alligator snapping turtle in eastern Texas, USA, May 2020–August 2021.

Ecological process	Covariate name	Description
Geographic location	Watershed	River mainstem the site is associated with.
	Latitude	Y-axis geographic coordinate in decimal degrees (World Geodetic System 1984 datum) of each site.
	Longitude	X-axis geographic coordinate in decimal degrees (World Geodetic System 1984 datum) of each site.
Characteristics of subwatersheds	Open water	Proportion of the U.S. Geological Survey (USGS) subwatershed defined as open water in the National Land Cover Database 19 (NLCD).
	Forest cover	Proportion of the USGS subwatershed defined as deciduous forest, evergreen forest, or mixed forest in the NLCD.
	Open cover	Proportion of the USGS subwatershed defined as pasture-hay or cultivated crop (i.e., agricultural land) in the NLCD.
	Developed cover	Proportion of the USGS subwatershed defined as developed open space, developed low intensity, developed medium intensity, or developed high intensity in the NLCD.
	Wetland cover	Proportion of the USGS subwatershed defined as woody wetlands or emergent herbaceous wetlands in the NLCD.
Local habitat characteristics	Dams	Number of dams between the survey site and the mainstem of its watershed.
	Sinuosity	Ratio of a water body's actual length contained by the most upstream and downstream traps to the linear distance between the same traps. 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 to approximate the degree of human visitation pressure a site receives.
	Veg	Proportion of traps within a site where we observed submerged or emergent vegetation.
	Floating veg	Proportion of traps within a site where we observed floating vegetation.
	Debris	Proportion of traps within a site where we observed emergent or submerged woody debris.
	Canopy	Average canopy cover percentage above traps set at a site.
	Depth	Average water depth of traps set at a site.
Detection	Temp	Surface water temperature (°C)
	Flow	Surface flow velocity (m/sec) in the main channel of a trapped area.
	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 trap locations.

site *i* being occupied, to in turn estimate occupancy probability (Ψ). The latent state variable *z* is also binary. Covariates were incorporated with a logit link function. Three assumptions pertinent to consider with this study's sampling methods are implicit in this occupancy model. The first is that occupancy status (z_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 alligator snapping turtles to adopt home ranges they move from infrequently (Trauth et al. 2016). Second is the assumption of 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 it is inevitable in the context of most ecological studies across areas where abundance varies (Royle and Nichols 2003, Dorazio 2007, Tanadini and Schmidt 2011). This highlights an important consideration when using this model (see Royle-Nichols *N*-mixture model below). Third, repeat surveys and sites are independent. Rebaiting traps between surveys minimized the risk of second and third survey outcomes depending on prior survey(s). Individuals that were caught in a trap on one survey were unlikely to be recaptured during subsequent surveys, however, which indicates there was a behavioral response negatively influencing *p* in secondary and tertiary surveys. Despite this behavioral response, there was no consistent pattern of decreasing counts with additional surveys (Appendix A). If dependence between surveys were occurring, it was not apparent in the counts of turtles of each survey. We initially accounted for inter-survey dependence with a binary dummy covariate of *p*, which we assigned a value of 0 for primary surveys and 1 for subsequent surveys (MacKenzie et al. 2006). This did not exhibit a strong negative relationship with detection data, so we assumed dependence was negligible and did not consider this covariate. Each site was sufficiently spaced to prevent one site's occupancy status to directly influence another's (i.e., no exchange of individuals between sites), and we assumed other potential sources of spatial dependence in occupancy were accounted for by covariates.

We assessed the absolute fit of the global model representing each of the 3 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 the species is truly absent at a site, we 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

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). We fitted detection and nondetection survey data to the model described by Royle and Nichols (2003), which accounts for variation in *p* resulting from variation in *N*. Despite shortcomings of this model (Barker et al. 2018, Link et al. 2018; see multinomial *N*-mixture model below), using it allowed inference on whether *p* is density dependent in hoop trap surveys (Linden et al. 2017), and determination of whether detection and nondetection data alone are sufficient to estimate alligator snapping turtle expected abundance (λ) and relative abundance by comparison with model-estimated values that use count data. Because we modeled abundance as a Poisson distribution, we incorporated its covariates with a log link function. Assumptions of this model are similar to those of the static site occupancy model (Doré et al. 2011). We 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 our dataset of individual detections, we used 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 the alligator snapping turtle 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, we simply identified them and did not count them (Appendix A). With a maximum of 3 surveys/site, each individual at a site had 4 potential detection histories: 1 - -, 01 -, 001, or 000. Because there were >2 detection outcomes, the observation process was multinomial (Kéry and Royle 2016). Using this model enabled comparison with the Royle-Nichols (RN) and occupancy models to determine whether coarser detection and 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).

Binomial *N*-mixture models (including RN models), which do not require the identity of surveyed individuals to be known, rely on assumptions that may limit their use (Barker et al. 2018, Link et al. 2018). Analogous to occupancy models, they assume stasis in population size (i.e., no emigration or immigration) at each site for the duration of sampling, and that there is no unaccounted variation in detection probability among visits (Kéry and Royle 2016, Barker et al. 2018, Link et al. 2018). Because binomial *N*-mixture models do not incorporate information on individual identity, they also require the assumption that an individual encountered during a given survey is counted only once during that survey (Link et al. 2018). As described by Dennis et al. (2015), they require specification of a constant *K*, which is often arbitrary and to which resultant abundance estimates are sensitive. Depending on *K*, abundance estimates may be unreasonably large or infinite (Barker et al. 2018).

By tracking the identity of individuals across each sampling occasion and incorporating this information into a multinomial model of the observation process, we confirmed that each individual was only counted once, and did not have to specify *K* to estimate abundance. Nevertheless, use of the multinomial *N*-mixture model does rely on assumptions of no dispersal and no unmodeled heterogeneity in detection similar to the binomial *N*-mixture model (Dorazio et al. 2005). The assumption of no immigration and emigration across surveys was reasonably met by the limited timeframe over which repeat surveys occurred, and variation in detection probability was accounted for to the extent possible with site- and survey-specific covariates. Assessing abundance through a mark-recapture distance sampling framework was precluded on the basis of our sampling design, in which detection was contingent on responsive movement of alligator snapping turtles into traps (Schmidt et al. 2022).

Preliminarily, we modeled abundance to follow a Poisson distribution. We determined the absolute fit of this model to the data 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 $\hat{c} > 2$. Thus, we modeled abundance as a negative binomial distribution (Kéry et al. 2005) 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). We 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. We used the formula described above (McArdle 1990) to calculate the number of surveys required to attain 95% confidence all alligator snapping turtles available for capture had been detected at a site (this does not consider the reality that over longer periods of survey time, the assumption of site closure is more likely to be violated).

We used Pearson's correlation coefficients (r) to determine correlations between λ estimated by the RN and multinomial N-mixture models and between Ψ estimates of the site occupancy model and λ estimates of the N-mixture models. We also assessed differences in absolute counts given by the 2 N-mixture models with least-squares regression (Linden et al. 2017).

RESULTS

Our sampling in 2020 and 2021 yielded 2,153 trap-nights at 51 sites in 42 counties. This effort resulted in 238 detections of 221 alligator snapping turtles and confirmed 60.7% of sites ($n = 31$) occupied. The highest number of captured turtles in a survey was 11, and the highest number of captures at one site was 17 (max. CPUE = 0.378; Appendix B). Of the 48 sites analyzed, overall CPUE was 0.105 turtles/trap-night, with an average per-site CPUE of 0.094. Southwestern and northeastern watersheds exhibited the lowest average capture rates (Figure 1). No global model indicated significant overdispersion (Appendix C).

Site occupancy model

Mean p (i.e., not considering site and survey heterogeneity) was estimated to be 0.77 (95% CI = 0.66, 0.85). Under constant conditions, approximately 2 surveys (95% CI = 2, 3) would be required for 95% confidence of alligator snapping turtle 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 the variance inflation factor of all detection covariates was <3.6 in the global site detection submodel, we retained all covariates. Detectability of the species decreased with increased flow velocity ($\beta_{flow} = -0.99$, 95% CI = −1.77, −0.21) and increased trap NND ($\beta_{NND} = -1.80$, 95% CI = −3.01, −0.59). Odds ratios indicated decrease in detection by a factor of 0.33 for every standardized unit increase of flow velocity (i.e., for every 0.34 m/sec increase) and decrease in detection by a factor of 0.38 for every standardized unit increase in NND (i.e., 179.4 m). Lunar phase also affected p ($\beta_{lunar}^2 = 1.33$, 95% CI = 0.54, 2.12; Table 3; Figure 2). Detection probability decreased 57.3% from 0.91 near new moons to 0.39 near full moons when other covariates were at mean observed values. After accounting for heterogeneity in p, mean $\hat{\Psi}$ 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 variance inflation and standard errors for all models of occupancy and abundance. Therefore, we considered only latitude and longitude as geographic location covariates. Estimated occupancy probability 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 (Figure 1). Estimated occupancy probability 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 3). Of the subwatershed hypotheses considered, forest cover alone was the best predictor of species occupancy ($\beta_{forest} = 2.89$, 95% CI = 0.53, 5.25; Table 3; Figure 2). The odds ratio indicated an increase by a factor of 18.04 for every 1 standardized unit (i.e., 44%) increase in subwatershed forest cover. Neither proportion of wetland cover nor developed land cover were competitive predictors of occurrence on their own. Agricultural land, however, was negatively correlated with forest cover ($r = -0.55$), and consequently also exhibited a moderate negative relationship with Ψ ($\beta_{open} = -0.92$, 95% CI = −1.88, 0.040). All local stream habitat variables were poor predictors of occupancy (Table 3). Relationships between Ψ and all considered local habitat variables were estimated to be positive, but standard errors were too large to warrant predictive use or inference.

TABLE 3 Models of alligator snapping turtle site occupancy (Ψ) with difference in Akaike's Information Criterion corrected for small sample size (ΔAIC_c) < 2. We fitted models with data from 48 locations within eastern Texas, USA, sampled from May 2020–August 2021. All models with covariates of occupancy include detection (p) covariates from the most supported detection model. K = number of model parameters, w_i = Akaike weight, and LL = log-likelihood.

Model[a]	K	AIC_c	ΔAIC_c	w_i	LL
Detection 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 models					
Ψ(latitude + latitude^2 + longitude)	9	129.78	0.00	0.99	−53.52
Subwatershed models					
Ψ(forest)	7	132.88	0.00	0.54	−58.04
Local habitat models					
Ψ(.)	6	143.28	0.00	0.49	−64.62
Ψ(canopy + debris)	8	144.36	1.08	0.28	−62.33

[a]Flow refers to surface water flow velocity in the main channel of a trapped area; lunar refers to the state of the moon along the lunar cycle (in radians) during a survey; NND refers to average nearest neighbor distance of trap locations; date is ordinal day of the year; temp is surface water temperature; latitude is the Y-axis geographic coordinate in decimal degrees; longitude is the X-axis geographic coordinate in decimal degrees; forest is the combined proportion of deciduous forest, evergreen forest, and mixed forest cover within the subwatershed; canopy refers to average canopy cover percentage above traps deployed at a site, debris is the proportion of traps within a site where we observed emergent or submerged woody debris.

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; Figure 3). Accounting for covariate standardization, odds ratios for flow velocity and NND indicated decreases in individual detection probability by a factor of 0.56 for every 0.34 m/sec increase in flow velocity, and by a factor of 0.29 for every 179.4-m increase in trap NND. Individual detection probability was highest near new moons (0.84) and decreased by 81.43% to 0.16 near full moons when other covariates were at mean observed values. 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 4) and lower relative $\hat{c}$ in global RN models with abundance covariates (Appendix C). The mean probability of individual detection (i.e., without accounting for covariate influences) was 0.65 (95% CI = 0.48, 0.78).

Detection and nondetection data underestimated counts of turtles. Expected abundance in the null RN model was 1.03 turtles (95% CI = 0.69, 1.55), and because of 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 imperfect detection, abundance patterns were congruent with those shown by CPUE, in which counts varied unimodally over a latitudinal gradient (Figure 1; Table 4). The relationship between latitude and abundance was stronger than with occurrence ($\beta_{latitude}{}^2$ = −0.83, 95% CI = −1.36, −0.30). Abundance was predicted to be highest at 31.58° latitude, decreasing by 62.13% at 33° in the Mississippi watershed and by 68.68% at 30° in proximity to the lower Trinity and San Jacinto watersheds (Figure 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). With a relatively low w_i, the RN model indicated that forest cover did not have as great an

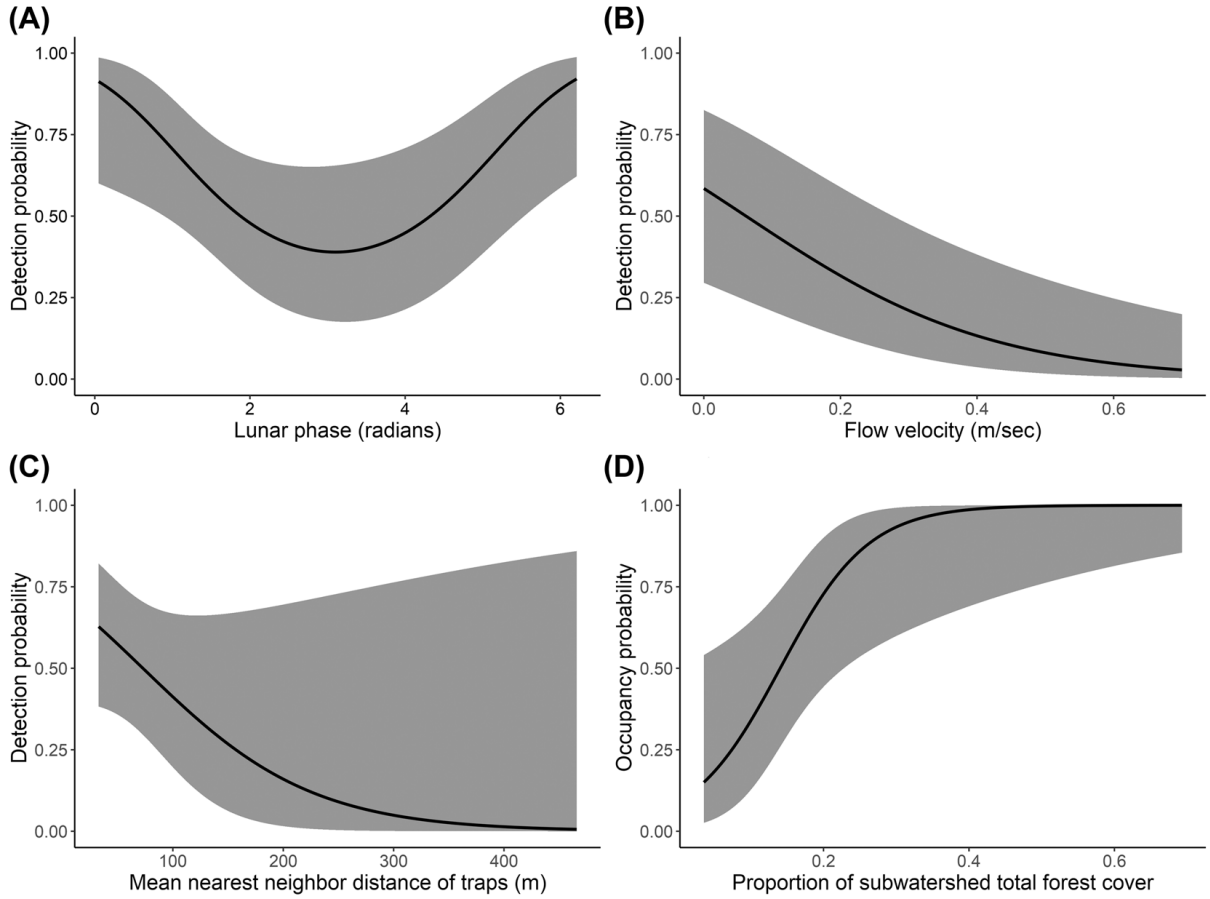

FIGURE 2 Predicted alligator snapping turtle occupancy probability and detection probability from the top-ranked subwatershed occupancy model using survey data collected in eastern Texas, USA, May 2020–August 2021. A) Alligator snapping turtle detectability is predicted to increase at new moons (0 and 6.28 radians), and decrease near the full moon (3.14 radians). B) Increasing flow velocity and C) trap nearest neighbor distance (NND) lowered detection probability. Although NND was included in the most supported 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.

influence on abundance as on occurrence. Forest cover abundance decreased by 71.53% from 50% cover to 10% cover, which corresponded to 3.74 to 1.06 turtles, respectively. As proportion of forest cover increased, the modeled rate of change in abundance also increased; for example, the number of predicted turtles at 70% forest cover (5.11 individuals) decreased by 26.95% at 50% forest cover (3.74 individuals). Local habitat variables were poor predictors of abundance, furthering the similarities in inferences produced by analyses of occupancy and abundance.

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. Six surveys (95% CI = 4, 9) would be required for 95% confidence that all individuals available for capture are detected at a site. Water temperature was eliminated from multinomial detection submodels (variance inflation factor > 5). Flow velocity, lunar phase, and trap NND were important determinants of individual detection. The contribution of trap spacing to detectability, however, was greater than indicated by the RN model, and while lunar

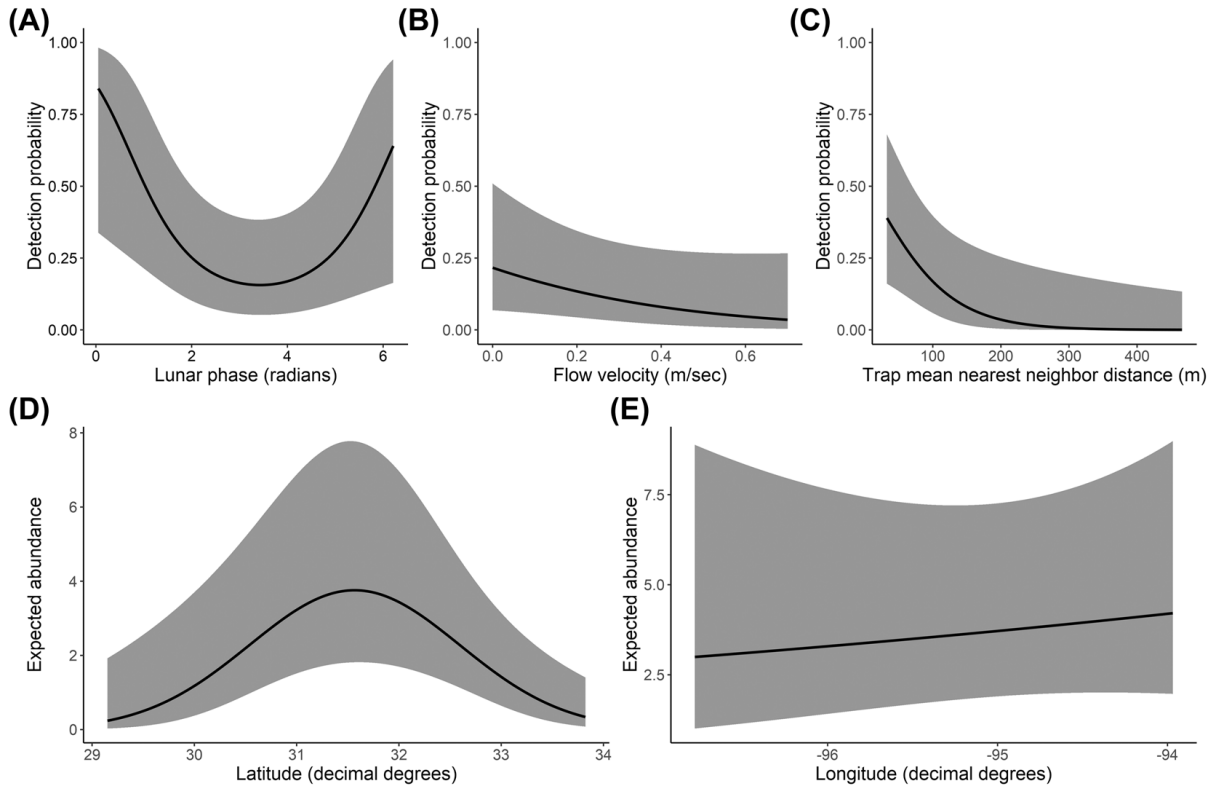

FIGURE 3 Predicted individual alligator snapping turtle detection probability and abundance based on the top-ranked Royle-Nichols *N*-mixture model using survey data collected in eastern Texas, USA, May 2020–August 2021. A) Detection probability is predicted to be highest during new moons (0 and 6.28 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 because of large confidence intervals. Gray shading depicts 95% confidence intervals.

phase was fitting as a predictor of species detection, it had less of an effect on numbers detected relative to other variables (Table 5). The top model included flow velocity ($\beta_{flow} = -1.01$, 95% CI = −1.62, −0.41) and trap NND ($\beta_{NND} = -1.41$, 95% CI = −2.25, −0.57) as covariates (Figure 4). Accounting for covariate standardization, odds ratios indicated a decrease in individual detection probability by a factor of 0.45 for every 0.34 m/sec increase in flow velocity, and a decrease by a factor of 0.31 for every 179-m increase in trap NND.

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. 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 5) despite the RN model overestimating detection and underestimating λ. Abundance was predicted to be highest at 31.45° latitude, with similar decreases to the north and south (70.49% and 66.66% decreases to 33° and 30° degrees, respectively) as those predicted by the RN model. Forest cover was not a reliable predictor ($\beta_{forest} = 0.25$, 95% CI = −0.20, 0.69; Figure 4). Average density 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 0.931 km, resulting in an estimated density of 8 individuals/channel km.

Using the top ranked multinomial *N*-mixture model (Table 5), $\hat{N}_i$ of alligator snapping turtles present during surveys ranged up to 28 individuals, 11 more than the maximum number observed at any site (Appendix B). Expected abundance trended positively with CPUE. Ranking sites according to increased counts of individuals using CPUE, however, did not lead to the same site ordering as when using $\hat{\lambda}$ (Appendix B).

TABLE 4 Royle-Nichols *N*-mixture models of alligator snapping turtle abundance (λ) and detection (*r*) probability with Akaike's Information Criterion corrected for small sample size (ΔAIC_c) < 2. We fitted models with data from 48 locations within eastern Texas, USA, from May 2020–August 2021. All models with covariates of abundance include detection covariates from the most supported detection model. *K* = number of model parameters, w_i = Akaike weight, and LL = log-likelihood.

Model[a]	*K*	AIC_c	ΔAIC_c	w_i	LL
Detection 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 models					
λ(latitude + latitude^2 + longitude)	9	133.52	0.00	0.96	−55.39
Subwatershed 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 models					
λ(.)	6	140.51	0.00	0.45	−63.23
λ(HAI)	7	142.34	1.83	0.18	−62.77

[a]Flow refers to surface water flow velocity in the main channel of a trapped area; lunar refers to the state of the moon along the lunar cycle (in radians) during a survey; NND refers to average nearest neighbor distance of trap locations; date is ordinal day of the year; temp is surface water temperature; latitude is the Y-axis geographic coordinate in decimal degrees; longitude is the X-axis geographic coordinate in decimal degrees; forest, wetland, developed and crops are the proportion of these cover types within a subwatershed; HAI (human accessibility index) is an index based on observations approximating the degree of human visitation pressure a site received.

The 3 model types ranked the relative importance of variables and the direction of their effects on occupancy and abundance similarly, with the exception of habitat covariates with high standard errors. Abundance was not predicted as well as occurrence by land cover covariates when count data were used. 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 (Figure 5). The relationship between estimated abundances of the 2 model types was modeled linearly as $\hat{\lambda}_{i\,(multinomial)} = 0.44 + 3.308\ \hat{\lambda}_{i\,(RN)}$ with $R^2 = 0.94$. The occupancy and the multinomial $\hat{\lambda}$ estimates were positively correlated ($r = 0.78$).

DISCUSSION

In eastern Texas, the alligator snapping turtle is likely to occupy the majority of large, permanent waters within watersheds it inhabits, as indicated by the high mean occupancy probability. The overall estimated density of approximately 8 individuals/channel km across these waters is lower than has been estimated from long-term population studies in Georgia (14 individuals/km; Folt et al. 2016) and Oklahoma, USA (28 and 68 individuals/km; Riedle et al. 2008*b*). The estimate in our study, however, is fundamentally different. Specifically, it is an average over all sites in the study area (across the meta-population; Kéry and Royle 2016), even those where the species is estimated to be absent, as opposed to an estimate based on intensive sampling of 1 population. Variation in both occupancy and abundance of the species were better

TABLE 5 Multinomial *N*-mixture models of alligator snapping turtle abundance (λ) and detection (*p*) probability with Akaike's Information Criterion corrected for small sample size (ΔAIC_c) < 2. We fitted models with data from 48 locations within eastern Texas, USA, sampled from May 2020–August 2021. All models with covariates of abundance include detection covariates from the most supported detection model. *K* = number of model parameters, w_i = Akaike weight, and LL = log-likelihood.

Model[a]	*K*	AIC_c	ΔAIC_c	w_i	LL
Detection 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 models					
λ(latitude + latitude^2 + longitude)	8	47.14	0.00	0.91	−13.73
Subwatershed models					
λ(.)	5	51.90	0.00	0.33	−20.23
λ(forest)	6	53.31	1.41	0.16	−19.63
Local habitat models					
λ(.)	5	51.90	0.00	0.54	−20.23

[a]Flow refers to surface water flow velocity in the main channel of a trapped area; NND refers to average nearest neighbor distance of trap locations; lunar refers to the state of the moon along the lunar cycle (in radians) during a survey; latitude is the Y-axis geographic coordinate in decimal degrees; longitude is the X-axis geographic coordinate in decimal degrees; forest is the combined proportion of deciduous forest, evergreen forest, and mixed forest cover within a subwatershed.

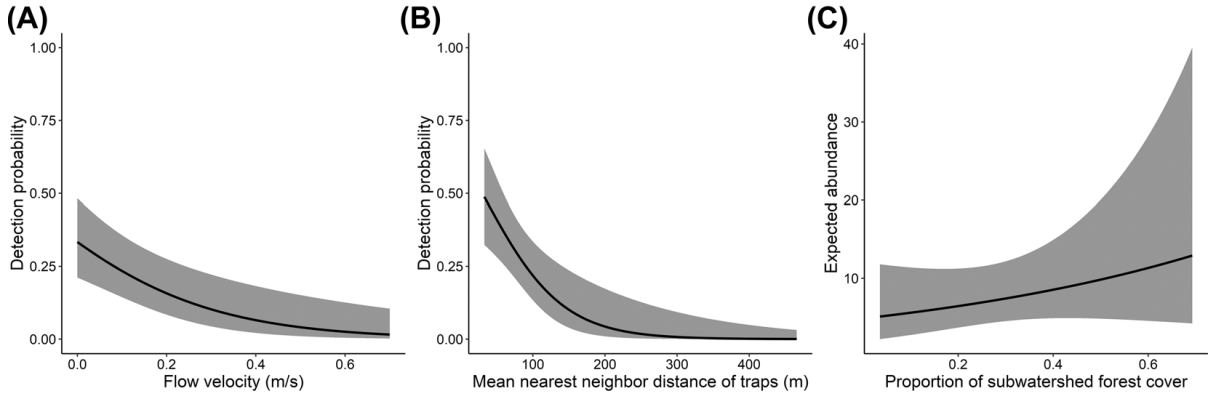

FIGURE 4 Predicted individual alligator snapping turtle detection probability and abundance based on the top-ranked multinomial *N*-mixture model using survey data collected in eastern Texas, USA, May 2020–August 2021. Gray shading depicts 95% confidence intervals. A) Flow velocity and B) mean nearest neighbor distance of traps were inversely correlated with detection. C) Increased subwatershed forest cover positively correlated with abundance, yet owing to large confidence intervals, predictive inference using this variable is limited.

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 effects 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,

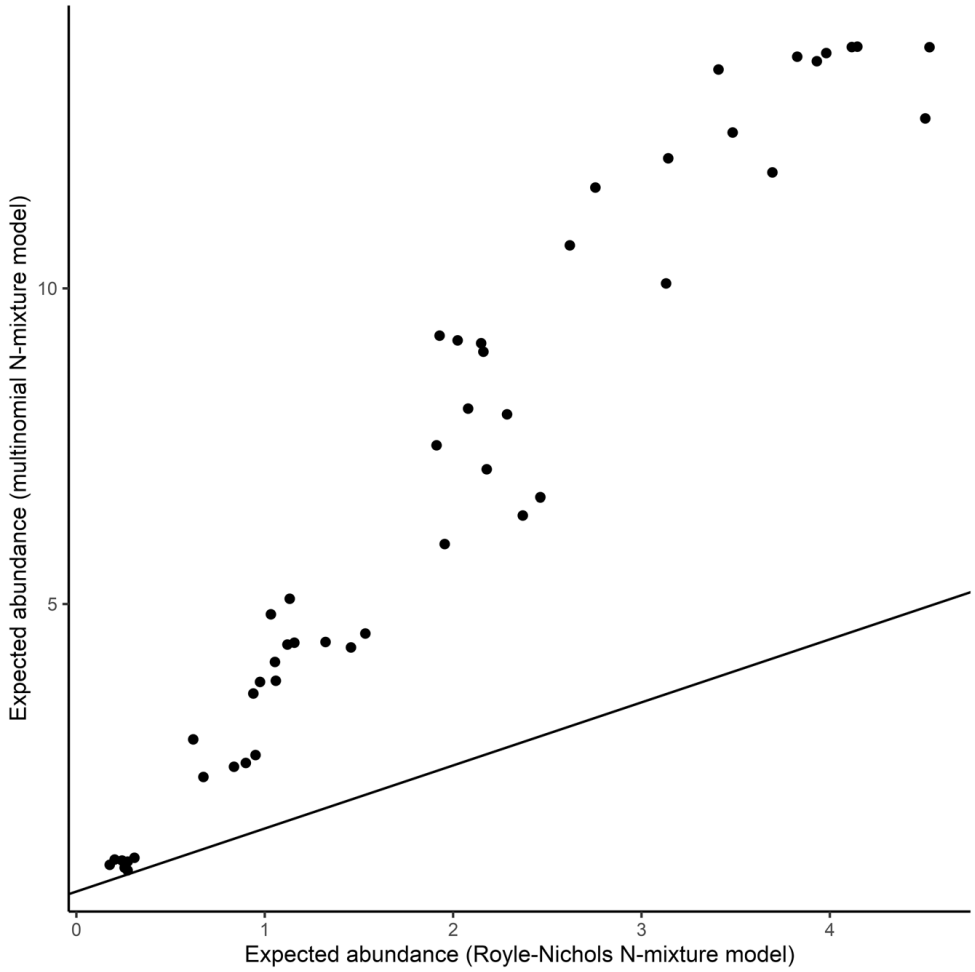

FIGURE 5 Estimated alligator snapping turtle abundances for the best-fit Royle-Nichols *N*-mixture model (*x*-axis) and multinomial *N*-mixture model (*y*-axis) based on sampling efforts that took place in eastern Texas, USA, May 2020–August 2021. The solid line depicts a slope of 1. Although both models 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 abundance, with values often below counts of turtles actually observed (max. estimated = 4.53, max. observed = 17).

temperature and ordinal date were not strong determinants. Furthermore, these results suggest that CPUE underestimated the extent of alligator snapping turtle occurrence, and because of heterogeneity in detection probability across sites, would result in imprecise inferences if used as an index of relative abundance. Although the RN model revealed patterns in relative abundance across sites similar to those given by the multinomial model, detection and nondetection data consistently underestimated absolute abundance as determined by comparison to empirical count data and multinomial *N*-mixture model-estimated abundance (Figure 5; Appendix B). This corroborates the results of Barker et al. (2018) that show *N*-mixture models that do not account for the identity of individuals are unreliable for estimating absolute abundance.

Determinants of detection probability

Survey efforts confirmed that environmental heterogeneity leads to variation in alligator snapping turtle detectability. Specifically, trapping under conditions of high flow will underestimate abundance. The alligator snapping turtle is predominantly benthic, with limbs adapted to gripping (Harrel et al. 1996*b*). 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. 1996*a*) and to conserve energy that would be required for swimming. Furthermore, 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 and would reduce the amount of time bait emitted scent. Jensen and Birkhead (2003) suggested that lentic systems (i.e., waters with no flow) lead to lower detection probability of the alligator snapping turtle by reasoning that these systems cannot effectively disperse bait scent (Jensen and Birkhead 2003). Conversely, our 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*.

In accordance with the hypothesis that increased water volumes decrease trap effectiveness, increased trap spacing decreased detections of alligator snapping turtles. 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 affects detection of other species. For example, in a study on tiger (*Panthera tigris*) abundance, Wegge et al. (2004) reported that greater distances between motion-sensitive cameras reduced detections. Trap spacing is more important for determining alligator snapping turtle abundance than for confirming occupancy, however. Increasing trap density (i.e., reducing the area of aquatic habitat covered) in occupied habitat may be efficient for capturing more individuals, and we recommend that future survey efforts standardize and report inter-trap distances.

Detection of alligator snapping turtles 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 (Baldwin and Lofton 1959, Davis and Whiting 1977, Bernardo and Plotkin 2007, Pinou et al. 2009), 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). Conversely, Kot et al. (2009) noted lunar periodicity of loggerhead sea turtle (*Carretta carretta*) and leatherback sea turtle (*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 the alligator snapping turtle 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, or turtles being better able to see fishes (Drummond and Gordon 1979). Foraging efficiency of fishes increases under increased irradiance (McMahon and Holanov 1995, Fraser and Metcalfe 1997). 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. We observed individuals entering traps diurnally on 3 occasions, however, indicating that scavenging takes place even under well-lit conditions. Water turbidity is another factor that interacts with light in foraging dynamics of aquatic organisms (Benfield and Minello 1996). The quadratic relationship between alligator snapping turtle 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, neither date nor temperature were reliable predictors of detectability. Nevertheless, temperature does affect both alligator snapping turtle habitat selection and activity (Riedle et al. 2006, Fitzgerald and Nelson 2011). 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). Because of these factors, Munscher et al. (2020) postulated that alligator snapping turtle 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 alligator snapping turtles occupying a similar climate in Louisiana, USA. In our study, however, individuals entered traps when surface water temperatures were at the minima recorded across all surveys: 13.3°C (early Mar 2021) and 14.2°C (early Apr 2021). Individuals

also entered traps while surface temperature was 29.0°C (late Jun 2020), which was within one degree of the maximum temperature recorded in the study. We detected individuals from March through September, but had we allocated survey efforts to late autumn and winter as well, greater ranges in date and temperature may have made the variables stronger predictors of detectability.

The high mean species detection probability (0.77) from the site occupancy model quantifies the efficacy of hoop trapping as a sampling method, although other chelydrid hoop trap surveys have noted lower detection rates. Common snapping turtles in Rhode Island, USA, and alligator snapping turtles in Oklahoma and Louisiana exhibited mean detection probabilities of 0.40 (Buchanan et al. 2019) 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 species 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 species detectability exhibited from the locales surveyed in these states may indicate lower mean abundance than sites surveyed in Texas.

Determinants of distributional patterns

Catch per unit effort did show a clear latitudinal pattern in relative abundance across the study area, which was corroborated after quantifying false-negative error rate. This suggests that alligator snapping turtle hoop trap surveys standardized only by use of CPUE (Folt and Godwin 2013, Lescher et al. 2013, King et al. 2016, Huntzinger et al. 2019) are capable of capturing general patterns in relative abundance, albeit with biases that arise from other sources of inter-survey and inter-site heterogeneity. Our data provide little support that abundance of the species declines at longitudes closer to its western range edge in the state. Because the western range boundary of the species is in Texas, a positive relationship between longitude and occurrence and abundance is inherent. The low magnitude of the relationship within the study area 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.

Among the considered subwatershed variables, forest cover was the strongest predictor of alligator snapping turtle occurrence and abundance, whereas decreased occurrence probability and abundance in developed and agricultural landscapes were not strongly supported. There are several reasons why forest cover could predict occurrence of the species. First, the zone of high forest cover in eastern Texas could simply represent a climatic zone that delineates the range of the species. 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 alligator snapping turtle's preferred habitat (Griffith et al. 2007), which would in turn increase its dispersal potential throughout aquatic habitats of these watersheds.

There is also evidence the alligator snapping turtle 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, Allan et al. 1997, Wang et al. 2003), and large-scale forest cover is associated positively with instream habitat variables that are important to the ecology of the species (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 buffer forest cover provides to bottomland swamps and water bodies (Booth et al. 2002). Considering known microhabitat preferences of alligator snapping turtles 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 effect of these cover types within the study area, decreases in forest cover influenced 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 we sampled, it appears that the alligator snapping turtle 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 alligator snapping turtle occupancy and abundance are a result of shared climatic limitations. As mentioned above, however, there is evidence that the species selects microhabitats (Riedle et al. 2015) 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. 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 alligator snapping turtle occupancy (Johnson 2020).

The relative lack of explanatory ability of these variables in Texas and Louisiana is likely an artifact of trapping methodology. First, we measured habitat variables in the vicinity of each trap, so they may not holistically quantify the abundance of suitable microhabitat within each site. Closely related to this supposition is that turtles could be actively attracted to trap vicinities from other locations. When foraging or dispersing, individuals may use 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 we sampled negatively affected turtle abundance. Nevertheless, even the lotic sites we visited with low sinuosity exhibited some sheltered low-energy pools and bends. Expanding the range of habitats sampled (e.g., allocating greater representation of channelized urban habitats) may support a positive relationship between abundance and sinuosity (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, and Trinity river lowlands consist of similar habitat intersecting the Blackland Prairie ecoregion (Griffith et al. 2007), and natural populations of the alligator snapping turtle are only known to occur in the latter system (Rosenbaum et al. 2023). The lack of the species in the former 2 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 locations such as a reservoir in the desert of central Oregon, USA (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 areas but do not necessarily apply to population persistence.

Overall, the alligator snapping turtle is likely to occur in the majority of waters in the study area, assuming sampled sites are representative of this region. 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.

The notable 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 nebulous. Notably, some subwatersheds

surrounding the Red River where we failed to detect the species have high forest cover. Because this region contains suitable land cover 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.

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. Using only detection and 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 (Doré et al. 2011, Linden et al. 2017, Ward et al. 2017), despite the RN model underestimating abundance relative to empirical counts. Our study showed 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 alligator snapping turtle abundance is influenced by additional environmental variables to those dictating distribution (Ward et al. 2017).

RESEARCH IMPLICATIONS

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 the alligator snapping turtle, for which occupancy surveys will be ineffective at detecting population declines even if separated by decades. Our study confirms the need for uniform standardization in alligator snapping turtle surveys, and the need for 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. Subsequent large-scale studies of the species that calculate mean abundance across sites while quantifying false-negative error rate would enable reliable comparisons across states where it occurs. This would streamline holistic, range-wide assessments of the species with minimal confounding biases between studies. Evidence for the influence of subwatershed forest cover on alligator snapping turtle occurrence and abundance, corroborated by the effects of subwatershed cover on fish communities reported from other studies, highlight a need to consider watershed effects 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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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animal handling and welfare during this study was compliant with a Texas Parks and Wildlife Department Scientific Permit for Research (SPR-0519-087) and Stephen F. Austin State University Institutional Animal Care and Use Committee project approval number 2019-11.

DATA AVAILABILITY STATEMENT

Data collected and analyzed as part of this study are available on request from the Texas Parks and Wildlife Department's Texas Natural Diversity Database. Information and instructions for accessing these data is available on: https://tpwd.texas.gov/huntwild/wild/wildlife_diversity/txndd/.

R Code used for data analysis is included as part of the online publication in Supporting Information.

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APPENDIX A: COUNT HISTORIES.

(See Table A1)

TABLE A1 Count histories of alligator snapping turtles for surveys (y) at 48 sites in eastern Texas, USA, used in occupancy and abundance models. Surveys occurred between May 2020 and August 2021. Integers listed after + indicate number of recaptures during respective surveys, which we did not use in multinomial N-mixture models. To protect locations of species occurrence, sites are identified by numbers. NA denotes that a survey did not occur.

Site ID	y_1	y_2	y_3	Site ID	y_1	y_2	y_3
1	11	1 + 1	5	25	0	0	0
2	4	1	4	26	0	0	NA
3	0	0	0	27	11	1 + 2	1
4	0	0	0	28	0	0	0
5	0	0	0	29	0	0	1
6	0	0	0	30	6	0	1 + 1
7	0	0	0	31	0	0	0
8	1	1	0	32	4	5	1 + 1
9	1	0	2	33	0	0	0
10	7	3	1 + 1	34	0	0	0
11	7	5 + 1	3 + 1	35	0	NA	NA
12	0	1	0	36	0	0	2
13	0	0	0	37	1	1	1
14	0	0	0	38	3	0	1
15	0	0	0	39	0	1	0
16	0	0	0	40	2	4	1
17	0	0	0	41	7	2 + 3	2
18	0	0	0	42	2	0	0
19	4	2	1	43	1	2	0
20	1	2	2	44	1	0	1
21	6	8 + 1	2	45	7	0	2 + 1
22	7	3	6	46	0	NA	NA
23	3	1	1	47	1	1	1 + 1
24	0	0	1	48	8	2 + 1	2 + 1

APPENDIX B: MODEL AND CATCH PER UNIT EFFORT COMPARISONS.

(See Table B1)

TABLE B1 Comparison of alligator snapping turtle catch per unit effort (CPUE) with expected abundance ($\hat{\lambda}_i$) calculated from the top-ranked multinomial *N*-mixture model, and with empirical Bayes' count estimates ($\hat{N}_i$), which are conditional on the observed data and estimates of $\hat{\lambda}_i$ and detection probability (p). We collected data used to calculate catch per unit effort and fit models from May 2020–August 2021 in eastern Texas, USA. The widest confidence intervals occurred at locations at middle latitudes and extremes of longitude within the study region. Watersheds are ordered from southwest to northeast.

Watershed and site ID	CPUE	$\hat{N}_i$	$\hat{N}_i$ 95% CI	$\hat{\lambda}_i$	$\hat{\lambda}_i$ 95% CI
San Bernard					
4	0	0.612	0–3	0.864	0.167–4.457
Brazos					
6	0	8.167	0–31	9.250	3.675–23.280
46	0	3.030	0–12	4.837	1.954–11.974
18	0	1.728	0–8	9.175	4.168–20.197
5	0	0.369	0–2	0.947	0.198–4.531
San Jacinto					
16	0	0.408	0–2	2.853	1.001–8.133
37	0.067	3.642	3–6	8.093	4.496–14.567
45	0.237	17.047	11–26	5.083	2.227–11.602
44	0.044	2.327	2–4	8.995	4.779–16.933
Trinity					
31	0	5.143	0–20	10.682	4.974–22.942
1	0.378	18.818	17–22	12.063	6.384–22.791
27	0.289	15.849	13–20	13.471	7.061–25.699
24	0.022	1.596	1–4	7.511	3.647–15.470
34	0	4.242	0–17	4.357	1.946–9.758
28	0	0.522	0–3	4.081	1.792–9.294
32	0.222	16.258	11–23	11.599	5.088–26.442
12	0.022	1.947	1–5	3.764	1.640–8.639
10	0.244	13.280	11–17	3.581	1.469–8.729
14	0	2.176	0–9	9.130	3.779–22.057
Neches					
29	0.022	12.607	2–35	13.827	7.626–5.071
36	0.044	3.468	2–7	13.824	6.403–29.850
40	0.178	8.231	7–11	13.602	7.617–24.291
41	0.244	13.066	11–17	10.078	4.785–21.229

(Continues)

TABLE B1 (Continued)

Watershed and site ID	CPUE	$\hat{N}_i$	$\hat{N}_i$ 95% CI	$\hat{\lambda}_i$	$\hat{\lambda}_i$ 95% CI
30	0.231	7.474	7–9	13.833	7.587–25.220
11	0.333	21.599	17–28	12.472	7.127–21.824
23	0.111	6.265	5–9	11.839	5.778–24.257
43	0.067	3.429	3–5	8.002	4.730–13.539
2	0.200	12.378	9–17	13.732	7.688–24.525
21	0.356	23.450	18–31	13.674	7.757–24.106
Sabine					
48	0.267	12.881	2–15	7.131	4.305–11.811
22	0.356	28.409	21–39	3.783	1.896–7.548
47	0.067	5.062	3–9	4.398	2.467–7.841
35	0	0.699	0–4	4.386	2.069–9.299
38	0.089	4.456	4–6	12.695	5.504–29.280
Mississippi					
3	0	1.313	0–6	2.479	1.042–5.902
15	0	0.510	0–3	0.914	0.275–3.040
19	0.156	13.360	8–21	6.404	2.909–14.094
7	0	0.112	0–1	4.311	2.277–8.164
33	0	0.037	0–1	0.776	0.217–2.769
20	0.111	5.807	5–8	6.689	3.066–14.592
13	0	0.551	0–3	2.257	1.009–5.050
17	0	0.254	0–2	0.932	0.243–3.569
42	0.044	2.362	2–4	5.951	3.382–10.471
25	0	0.609	0–3	0.819	0.239–2.800
8	0.044	2.299	2–4	4.532	2.409–8.526
26	0	0.094	0–1	0.975	0.310–3.069
9	0.067	6.168	3–12	2.605	1.098–6.181
39	0.022	1.720	1–4	2.419	1.074–5.449

APPENDIX C: FULL MODEL RESULTS.

(See Table C1)

TABLE C1 Complete list of models considered for determining occurrence and abundance of alligator snapping turtle across 3 spatial scales. Models within a cumulative weight of 0.95 (i.e., 95% confidence model set *sensu* Symonds and Moussalli 2011) are denoted with asterisks. Estimated overdispersion parameters ($\hat{c}$) are calculated and presented for each global model, as are probabilities that expected χ^2 is greater than or equal to the observed χ^2 in goodness-of-fit (GOF) tests (*P*). AIC_c = Akaike's Information Criterion corrected for small sample size, Ψ = occupancy probability, λ = expected abundance across sites, *K* = number of model parameters, w_i = Akaike weight, *p* = detection probability (species detection probability for occupancy models and individual detection probability for *N*-mixture models), and LL = log-likelihood. By convention, *r* is used to represent individual detection probability for Royle-Nichols models. Data used to fit models were collected from May 2020–August 2021 in eastern Texas, USA.

Model set and GOF test results	Model	*K*	AIC_c	ΔAIC_c	w_i	LL
Detection models[a]						
Static site occupancy (*P* = 0.304, $\hat{c}$ = 1.15)						
	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
	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 (*P* = 0.282, $\hat{c}$ = 1.20)						
	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
	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

(Continues)

TABLE C1 (Continued)

Model set and GOF test results	Model	*K*	AIC_c	ΔAIC_c	w_i	LL
	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 (*P* = 0.393, ĉ = 1.02)						
	p(flow + NND) λ(.)*	5	51.90	0.00	0.69	−20.23
	p(flow + lunar + $lunar^2$ + NND) λ(.)*	7	53.96	2.06	0.24	−18.58
	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
	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 state process models[b]						
Static site occupancy (*P* = 0.488, ĉ = 0.86)						
	Ψ(forest)*	7	132.88	0.00	0.54	−58.04
	Ψ(forest + developed)*	8	135.65	2.77	0.14	−57.98
	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 (*P* = 0.548, ĉ = 0.79)						
	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
	λ(forest + open)*	8	137.79	2.89	0.07	−59.05

TABLE C1 (Continued)

Model set and GOF test results	Model	*K*	AIC_c	ΔAIC_c	w_i	LL
	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 ($P = 0.323$, $\hat{c} = 1.07$)						
	λ(.)*	5	51.90	0.00	0.33	−20.23
	λ(forest)*	6	53.31	1.41	0.16	−19.63
	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 state process models[c]						
Static site occupancy ($P = 0.292$, $\hat{c} = 1.19$)						
	Ψ(latitude + latitude^2 + longitude)*	9	129.78	0.00	0.99	−53.52
	Ψ(.)	6	143.28	13.50	0.00	−64.62
	Ψ(latitude + longitude)	6	147.72	17.64	0.00	−66.83
Royle-Nichols *N*-mixture ($P = 0.504$, $\hat{c} = 0.82$)						
	λ(latitude + latitude^2 + longitude)*	9	133.52	0.00	0.96	−55.39
	λ(.)	6	140.51	6.99	0.03	−63.23
	λ(latitude + longitude)	8	143.31	9.79	0.01	−61.81
Multinomial *N*-mixture ($P = 0.245$, $\hat{c} = 1.14$)						
	λ(latitude + latitude^2 + longitude)*	8	47.14	0.00	0.91	−13.73
	λ(.)*	5	51.90	4.75	0.08	−20.23
	λ(latitude + longitude)	7	56.50	9.35	0.01	−19.85
Local habitat state process models[d]						
Static site occupancy ($P = 0.292$, $\hat{c} = 1.29$)						
	Ψ(.)*	6	143.28	0	0.49	−64.62
	Ψ(canopy + debris)*	8	144.36	1.08	0.28	−62.33

(Continues)

TABLE C1 (Continued)

Model set and GOF test results	Model	*K*	AIC_c	ΔAIC_c	w_i	LL
	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 ($P = 0.45$, $\hat{c} = 0.99$)						
	λ(.)*	6	140.51	0	0.45	−63.23
	λ(HAI)*	7	142.34	1.83	0.18	−62.77
	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
	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 ($P = 0.245$, $\hat{c} = 1.14$)						
	λ(.)*	5	51.9	0	0.54	−20.23
	λ(sinuosity)*	6	54.31	2.41	0.16	−20.13
	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

[a]Temp is temperature of surface water; flow refers to surface water flow velocity in the main channel of a water body; lunar is the state of the moon along the lunar cycle (in radians) during a survey; date is ordinal day of the year; NND is the average nearest neighbor distance of trap locations.

[b]Covariates are the proportion of the land cover type within a subwatershed.

[c]Latitude is the Y-axis geographic coordinate in decimal degrees; longitude is the X-axis geographic coordinate in decimal degrees.

[d]Sinuosity is the ratio of the actual length of a water body contained by the most upstream and downstream traps to the linear distance between the same traps; HAI (human accessibility index) is an index based on observations at each surveyed site to approximate the degree of human visitation pressure; debris is the proportion of traps within a site with emergent or submerged woody debris; depth is the average water depth of all traps set at a site; float. veg is the proportion of traps within a site with floating vegetation; veg is the proportion of traps within a site with submerged or emergent vegetation.