Capital to Coast: Primary Drivers of Distribution in the Secretive and Data-Limited Neuse River Waterdog (Necturus lewisi)

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The lack of demographic data for many protected species often means that threats are poorly understood during recovery planning, and this results in difficulty defining sufficient metrics for assessing progress on recovery actions. The Neuse River Waterdog (Necturus lewisi) is a federally protected aquatic salamander endemic to the Neuse and Tar-Pamlico River basins of central and eastern North Carolina. It has quietly declined during four decades of intense urbanization, but the specific drivers of decline are unclear because there are no demographic data and only limited detection/non-detection information available. Our first objective was to clarify the drivers of decline by synthesizing the current knowledge of the hypothesized threats to N. lewisi. Because preexisting demographic data are lacking, we used prior natural history research and studies of ecologically similar species to develop hypotheses for the observed declines in occurrence. Our second objective was to update the knowledge of the species’ current distribution throughout its historical range and then test our hypothesized threats using new occurrence data. We conducted detection/non-detection surveys across 116 locations throughout the species’ historical range in two consecutive winter seasons (2018–2019 and 2019–2020) and modeled the effects of local and landscape variables representing three broad threat categories (pollution, flow suppression, and land use/land cover) using an occupancy modeling approach. We fit models representing all biologically relevant combinations of variables simultaneously, recognizing that threats are not independent in their effect. Dominant substrate type was the best predictor of occurrence and was negatively associated with the transition from cobble to silt (P < 0.05). Our analysis most supported the hypothesis that observed declines in the occurrence of N. lewisi are a delayed result of sedimentation-induced recruitment limitation. Uncertainty in the mechanism of decline remains because recruitment limitation could not be directly estimated with two years of occurrence data, yet this interpretation gained through an understanding of the species’ underlying biology and current distribution contributes to the knowledge about present threats and will help guide and evaluate future recovery actions for this protected and narrowly endemic aquatic species.

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Natural Sciences (NCMNS) between 1979 and 1981 (Braswell and Ashton, 1985). Braswell and Ashton (1985) detected \( N. \text{lewisi} \) at 116 of 361 sites (32%) using presence-only surveys (i.e., surveys ended at first detection or after an arbitrary number of days with no detections; Fig. 1A). They predominantly used dipnetting and baited minnow traps for surveys as those methods were found to be the easiest and most effective (Braswell and Ashton, 1985).

Declines in species occurrence were first speculated in 2001 following a survey of Neuse basin sites impacted by new urbanization (Lambiase, 2001), but range-wide declines in occurrence were not observed until a second full-distribution monitoring survey was conducted by the North Carolina Wildlife Resources Commission (NCWRC) between 2011 and 2015. Biologists with the NCWRC led an inter-agency effort to resurvey most of the suitable historical NCMNS sites (\( n = 186 \)) using a similar methodology (i.e., presence-only surveys using ten baited minnow traps ended at first detection or after four days with no detections). They reported naïve site occurrence declines of approximately 40% in the Neuse River basin and approximately 30% in the Tar River basin when compared to the prior NCMNS survey results (NCWRC, 2015). Apparent site occurrence had declined predominantly in streams draining the Raleigh-Durham metropolitan area, throughout the main stem of the Neuse River, and in some small rural streams of both basins (NCWRC, 2015; Fig. 1B).

The United States Fish and Wildlife Service (USFWS) conducted a Species Status Assessment (SSA) in 2017 (USFWS, 2017) in response to the NCWRC survey results and a petition to list the species. Expert elicitation during the SSA identified a suite of threats to long-term species viability...
Our goal was to define broad threat categories that we possibly supported. The SSA analysis of the species’ current condition revealed that it was declining throughout a significant portion of its range, though the drivers remained unclear (Fig. 1C). *Necturus lewisi* was listed as “threatened” under the Endangered Species Act (ESA) in 2021, citing habitat degradation as the largest threat to persistence (USFWS, 2021).

The primary challenge for recovery planning is the lack of robust demographic data needed to confidently define and assess species resiliency, representation, and redundancy (Wolf et al., 2015; USFWS, 2019) in response to the hypothesized threats. Lack of data is a common conservation assessment and planning barrier for secretive and understudied species (Howard and Bickford, 2014; Kindsvater et al., 2018). Long-term demographic data would enable identification of the mechanisms driving declines by estimating vital rates (e.g., survival or movement) in response to specific threats, allowing for the development of quantifiable recovery metrics. Without long-term demographic data, however, inferences about the mechanisms driving declines must be obtained through other sources of information, such as expert opinion (Davis and Wagner, 2003; Fitzgerald et al., 2021), natural history information (Bury, 2006; Bland et al., 2013; Tucker et al., 2021), and data from similar species (Jarić et al., 2015; González-del-Pliego et al., 2019).

The mechanisms driving declines cannot be directly estimated using these alternative sources of information, but they can be evaluated indirectly using occupancy estimation. We considered occupancy estimation (MacKenzie et al., 2002) a logical first step in threat assessment and hypothesis testing for *N. lewisi* because we expected that changes in vital rates would lead to changes in realized occurrence (MacKenzie et al., 2017; Green and Bailey, 2020). This is a large assumption as stressors may affect vital rates like survival or recruitment without affecting occurrence patterns. Still, occurrence patterns that change in response to hypothesized threats may indicate which underlying mechanisms are driving observed declines. Following this reasoning allowed us to contribute a possible explanation for the observed range contractions of *N. lewisi* and to develop more targeted hypotheses with limited information.

The main objectives to this study were: (1) synthesize the current knowledge of hypothesized threats and their operating mechanisms, and to (2) update the knowledge of the current distribution of *N. lewisi* throughout its historical range by testing our hypothesized threats using new occurrence data. We could not explicitly test the mechanisms driving declines with occurrence data alone. However, we expected that estimating the relationships between occupancy probability and covariates associated with the hypothesized threats would allow us to infer which, if any, of our hypotheses were possibly supported.

**MATERIALS AND METHODS**

**Threat synthesis and hypothesis development**

Our goal was to define broad threat categories that we expected were responsible for driving the current distribution of *N. lewisi* by synthesizing information from natural history studies, studies with other large salamander species, and previously hypothesized threats (USFWS, 2017). We first identified a possible operating mechanism of decline that could be associated to each threat listed in the SSA (USFWS, 2017). Next, we developed hypotheses of how each operating mechanism, and by proxy, each listed threat, may be driving declines in observed occurrence. We then consolidated the listed threats into the broader threat categories of pollution, flow suppression, land use/land cover (LULC), biotic stress, and climate change based on the similarities among our hypotheses in each category (Table 1). The biotic stress and climate change threat categories may have been important to understanding the drivers of distribution, but they were not evaluated in this study. Data on the distributional extents of biotic threats, such as disease prevalence or non-native species that likely predate on *N. lewisi* (e.g., flathead catfish; *Pylodictis olivaris*), were not readily available. Climate change may threaten *N. lewisi* as flood and drought regimes change (USFWS, 2017), but these represent stochastic stressors with uncertainty in their future frequencies. Given our data limitations, we chose to only explore the threats associated with the recent, chronic changes to the study area and not stochastic climate-related threats.

The remaining three broad threat categories of pollution, flow suppression, and LULC revealed plausible hypotheses that might explain the previously observed declines in occurrence (NCWRC, 2015). Hypothesis 1: The pollution threat category, which includes pollution introduced by the threat of mining and energy production, would reduce local water quality in the downstream catchment. We hypothesized that reduced water quality would increase site-specific adult and juvenile mortality. Hypothesis 2: The flow suppression threat category would alter local habitat (e.g., sediment deposition or increased plant growth), alter local species assemblages (e.g., more fish predators), and reduce dissolved oxygen content. We hypothesized that the alterations caused by flow suppression would increase site-specific adult and juvenile mortality. Hypothesis 3: The LULC threat category, which includes intensive land uses like urbanization, agriculture, and forest management without proper best management practices (North Carolina Forest Service, 2021), would increase channel sedimentation. We hypothesized that sedimentation would reduce nesting habitat, thereby limiting site-specific recruitment. We tested these hypotheses by assuming that their effects on vital rates such as survival or recruitment could be estimated through realized changes in occupancy. We acknowledge this was a strong assumption that could not be verified in our evaluation, but it did allow us to begin exploring the drivers of occurrence with limited data.

**Current distribution: occupancy analysis**

**Survey design and data collection.**—We conducted a range-wide resurvey effort to assess the extant distribution of *N. lewisi* using a survey design that enabled estimation of site occupancy probability while accounting for imperfect detection (i.e., detection/non-detection; MacKenzie et al., 2002). We were interested in surveying both new and historically occupied sites throughout the potential range. We used a modified stratified sample design wherein we stratified potential survey sites by HUC10, predominant
Table 1. A synthesis of stressors expected to threaten long-term persistence of *N. lewisi*. All assumed threats, underlying mechanisms, and hypotheses were formed using support from prior work with phylogenetically and ecologically similar species, freshwater community studies, and our knowledge of the study area. The broad threat categories of pollution, flow suppression, and land use/land cover informed the suite of covariates estimated in our occupancy analysis and were used to generate the three primary hypotheses for the observed declines in occurrence. Hypothesis 1: Reduced water quality resulted in adult and juvenile mortality. Hypothesis 2: Altered local conditions caused by flow suppression resulted in adult and juvenile mortality. Hypothesis 3: Stream sedimentation has caused recruitment limitation.

<table>
<thead>
<tr>
<th>Broad threat category</th>
<th>USFWS identified threat</th>
<th>Underlying mechanism</th>
<th>Our hypothesis</th>
<th>Support</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pollution</td>
<td>Pollution</td>
<td>Chronically reduced water quality reduces prey species. Spill events result in mass die-offs.</td>
<td>Chronic water quality declines and toxic spills have contributed to reduced survival and local extirpations, particularly in urban areas, because <em>N. lewisi</em> is long-lived and has low dispersal abilities.</td>
<td>Pfingsten, 2013; Lambiase, 2001; Genito et al., 2002; Durflinger Moreno et al., 2006</td>
</tr>
<tr>
<td>Mining and energy production</td>
<td>Accidental spill events can result in local extirpations of aquatic fauna.</td>
<td>Toxic spill events can cause mass die-offs in <em>N. lewisi</em>.</td>
<td>Braswell and Ashton, 1985; Lemly, 2015; Cope et al., 2021</td>
<td></td>
</tr>
<tr>
<td>Flow suppression</td>
<td>Dams and barriers</td>
<td>Dams restrict population gene flow and impound sediment and flow.</td>
<td>Water impoundment is believed to contribute to local <em>N. lewisi</em> extirpations through hypoxia, but may also occur as a result of recruitment limitation from sedimentation.</td>
<td>Braswell and Ashton, 1985; Graham et al., 2014</td>
</tr>
<tr>
<td>Land use/land cover</td>
<td>Development</td>
<td>Increased surface runoff, channel erosion, and reduced baseflows in urban areas causes instability and homogeneity of natural benthic substrates.</td>
<td>Sedimentation reduces nesting site availability by filling interstitial spaces in the substrate, leading to recruitment limitation, reduced survival of young age classes, and gradual local extirpation.</td>
<td>Ashton, 1985; Helms et al., 2005; Quinn et al., 2013</td>
</tr>
<tr>
<td>Land use/land cover</td>
<td>Agriculture</td>
<td>Sediment and nutrient inputs from crop and livestock production reduce water quality and alter natural channel geomorphology.</td>
<td>Sedimentation reduces nesting site availability, limiting recruitment, and elevated nutrients reduce dissolved oxygen content and prey species richness, limiting adult and juvenile survival.</td>
<td>Ultsch and Duke, 1990; Genito et al., 2002; Wheeler et al., 2003</td>
</tr>
<tr>
<td>Forest management</td>
<td>Forest management</td>
<td>Surface runoff and channel erosion in recently logged areas causes instability and homogeneity of natural benthic substrates.</td>
<td>Sedimentation reduces nesting site availability, leading to recruitment limitation, reduced survival of young age classes, and gradual local extirpation.</td>
<td>Durflinger Moreno et al., 2006; Bodinof Jachowski and Hopkins, 2018; Kukułła and Bylak, 2020</td>
</tr>
<tr>
<td>Biotic</td>
<td>Invasive species</td>
<td>Non-native predators can have unbalanced interactions with resident prey species.</td>
<td>Waterdogs are limited in their behavioral response to non-native catfish and face increased predation.</td>
<td>Cope et al., 2019; Unger et al., 2021</td>
</tr>
<tr>
<td>Disease</td>
<td>Disease</td>
<td>Fungal and viral pathogens are common threats to aquatic amphibians in the eastern United States.</td>
<td>Diseases such as chytrid fungus and ranavirus have been found in ecologically similar species and may impact survival of <em>N. lewisi</em>.</td>
<td>Seeley et al., 2016; Hardman et al., 2020; Muse, 2020</td>
</tr>
<tr>
<td>Climate change</td>
<td>Climate change</td>
<td>Small stream channels may dry fully in severe droughts.</td>
<td><em>N. lewisi</em> cannot tolerate channel drying by behavioral or physiological means and become extirpated during such events.</td>
<td>Ultsch and Duke, 1990</td>
</tr>
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watershed land use, and prior survey data (NCWRC, 2015). This resulted in 116 unique sites spanning the species’ historical range. We surveyed 65 of the selected sites between November 2018 and March 2019. Between December 2019 and March 2020, we surveyed the remaining 51 unique sites and resurveyed 23 sites from the 2018–2019 season (~20% of all sites surveyed). We surveyed most sites on the upstream side of bridge crossings (94%) for ease of access, avoidance of potential road impacts, and to remain comparable to historical surveys.

We conducted surveys in two consecutive winter seasons when _N. lewisi_ are most active (Braswell and Ashton, 1985). In each season, we surveyed five to seven sites concurrently each week. At each site, we baited ten Gee’s Minnow Traps (1/4 in. mesh; Tackle Factory, Fillmore, NY) with chicken liver and placed them in the stream channel at 10 m intervals. We set traps on Monday and checked them daily until removal on Friday for a total of 40 trap-nights of effort per site. We immediately replaced lost traps during daily checks. Bait was secured in a punctured 4 oz plastic bottle and was not replaced unless the bottle or bait was lost. We collected water chemistry measurements daily and channel width measurements weekly at the first, fifth, and tenth trap of each site. Water chemistry parameters included water temperature (°C), pH, and conductivity (µS/cm) measured with an Extech EC500 meter and dissolved oxygen (mg/L) measured with an Extech DO600 meter (Extech Instruments, Nashua, NH). We measured wetted channel width (m) using a Halo XL450 Range Finder (GSM Outdoors, Irving, TX). We also conducted a rapid channel stability assessment at each site in 2020 using a modified U.S. Department of Transportation protocol (Johnson, 2006), where sites were scored based on weighted qualitative metrics. Qualitative metrics included: 1. Primary substrate category, 2. Presence of human-made bed/bank stabilization, 3. Degree of incision, 4. Degree of stream constriction, 5. Severity of bank erosion, 6. Relative percentage of each bank failing, 7. Relative percentage of 50 ft riparian buffer vegetated, 8. Relative percentage of bank with fluvial deposition, 9. Channel stage (disturbance level), 10. Substrate composition of adjacent side slope, 11. Relative percentage of side slope eroding and contributing to instream sediment, and 12. Relative severity of side-slope erosion. Sites could receive a maximum score of 47 points where low scores were considered more stable relative to high scores.

**Remotely sensed variables.**—We collected point feature data on National Pollutant Discharge Elimination System (NPDES) permitted sites, North Carolina Department of Environmental Quality (NCDEQ) macroinvertebrate community health, and North Carolina dams and barriers. NPDES permitted sites and NCDEQ macroinvertebrate community health assessment data were acquired from the NC OneMap geospatial data repository (North Carolina Department of Information Technology, 2019). We calculated the proportion of NPDES permitted sites within the watershed of each survey site (i.e., the number of NPDES sites divided by survey site watershed area) to estimate the site-specific effect of permitted point-source pollutants on the occurrence of _N. lewisi_. We chose this metric to measure the pollution threat category following prior speculation that an increase in NPDES permitted sites had decreased site occurrence of _N. lewisi_ (Lambiase, 2001). We also aggregated NCDEQ macroinvertebrate health scores from the nearest monitoring stations within the same HUC10 subbasins as our survey sites to estimate the site-specific effects of pollution, as indicated by the macroinvertebrate community, on occurrence of _N. lewisi_. We converted the descriptive scores to numeric values where 1 = Severe health, 2 = Poor health, 3 = Moderate health, 4 = Fair health, 5 = Good–Fair health, 6 = Good health, and 7 = Excellent health. Because the NCDEQ does not perform macroinvertebrate health assessments at every monitoring station every year, we used the most recent score available. If the most recent score available was assessed prior to January 2008 (i.e., > 10 years prior to our surveys), we chose the next nearest monitoring station that met our selection criteria. We used North Carolina dams and barriers data from the Southeast Aquatic Resources Partnership’s online Aquatic Barrier Prioritization Tool (SARP, 2022). We measured the stream distance (km) from each surveyed site to the nearest upstream or downstream dam to estimate the site-specific effect of dam presence on occurrence. We binned site distances to dams into classes from one (< 10 km to survey point) to ten (≥ 100 km to survey point or N/A), at 10 km increments, to accommodate sites without an upstream or downstream dam.

We sourced raster land cover data from the 2016 NLCD dataset (Dewitz, 2019) and reclassified it into five broader LULC types (i.e., developed, forested, herbaceous/pasture, agricultural crops, and wetland) to reflect variables relevant to our study. We corrected the overestimation of wetland LULC in 2016 NLCD dataset (Yang et al., 2018) by restricting wetland LULC boundaries to the National Wetlands Inventory polygon shapefile (USFWS, 2018) acquired from NC OneMap (North Carolina Department of Information Technology, 2019). All cells outside of the polygon boundaries were recategorized to forested LULC, thereby “shrinking” wetland to a more accurate proportion of the landscape. Typical approaches to estimating the effects of LULC on aquatic salamander occurrence measure the effects as the proportions of cover types within the watershed (Pugh et al., 2016; Bodinof Jachowski and Hopkins, 2018; Da Silva Neto et al., 2020) or within a defined buffer size around the stream (Surasinghe and Baldwin, 2015; Pugh et al., 2016; Wineland et al., 2019), chosen at a scale presumed critical to the species’ biology. We instead measured the effective proportion of each LULC type within the watershed using an inverse distance weighted approach, which calculates the cumulative hydrological contribution of each type relative to its position on the landscape. This approach allowed us to account for all LULC effects on water quality or stability within the watershed, while also recognizing that LULC near streams likely had a much higher relative effect than LULC far from streams. We calculated the effective proportion of each type using the hydrologically active inverse flow length to stream (HAIFLS) tool in the IDW-Plus ArcGIS custom toolset (Peterson and Pearse, 2017). We did not include LULC upstream from dams in our calculations because we assumed dams would curb LULC impacts downstream by impounding sediment and contaminants absorbed therein (Bednarek, 2001; Colas et al., 2011).

To account for differences in the ability to detect _N. lewisi_ during surveys, we collected daily weather covariates expected to influence detectability. Weather data were acquired from the North Carolina State Climate Office Cardinal Database (NCSCO, 2021). We collected minimum daily air temperature
Table 2. Covariates of detection probability and occupancy probability that were included in the global single-season occupancy model. The covariates of occupancy probability are visually subset in this table to illustrate the expected associations to the three broad threat categories of pollution, flow suppression, and land use/land cover (LULC).

<table>
<thead>
<tr>
<th>Detection $p$</th>
<th>Occupancy $\psi$</th>
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</thead>
<tbody>
<tr>
<td>Min daily air °C (Min daily air)$^2$</td>
<td>Hypothesis 1: Pollution</td>
</tr>
<tr>
<td>Precipitation (cm) (Precipitation)$^2$</td>
<td>NCDEQ benthic score</td>
</tr>
<tr>
<td>Season 1</td>
<td>Proportional NPDES</td>
</tr>
<tr>
<td>Distance to nearest upstream dam (km)</td>
<td>Hypothesis 2: Flow suppression</td>
</tr>
<tr>
<td>Distance to nearest downstream dam (km)</td>
<td>Distance to nearest downstream dam (km)</td>
</tr>
<tr>
<td>Channel stage</td>
<td>Hypothesis 3: LULC</td>
</tr>
<tr>
<td>(Channel stage)$^2$</td>
<td>Developed</td>
</tr>
<tr>
<td>Dominant substrate</td>
<td>Forested</td>
</tr>
<tr>
<td></td>
<td>Crop</td>
</tr>
<tr>
<td></td>
<td>Herbaceous/pasture</td>
</tr>
<tr>
<td>Season 2</td>
<td>Wetland</td>
</tr>
<tr>
<td></td>
<td>Developed*Wetland</td>
</tr>
<tr>
<td>Channel stage</td>
<td>Crop*Wetland</td>
</tr>
<tr>
<td>(Channel stage)$^2$</td>
<td>Developed*Crop</td>
</tr>
<tr>
<td>Dominant substrate</td>
<td>Developed*Pasture</td>
</tr>
<tr>
<td></td>
<td>Crop*Pasture</td>
</tr>
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and precipitation (cm) data during our surveys from the nearest available weather station within a 30 km radius of the survey site.

Linking variables to hypothesized threats.—We grouped field-collected and remotely sensed occupancy covariates by their expected associations to the threat categories (Table 2). We expected the effects of NPDES permitted sites and NCDEQ macroinvertebrate community health scores to explain the variation in site occupancy caused by the pollution threat category. We expected the effects of proximity to dams, dominant substrate type, and channel stage to explain the variation in site occupancy caused by the flow suppression threat category. The dominant substrate type and channel stage metrics were taken directly from the rapid channel stability assessments performed in 2020. We included a quadratic effect of channel stage because channel stability is maximized at both low channel stages (i.e., a natural stream channel) and high channel stages (i.e., pseudo-equilibrium following chronic disturbance). Lastly, we expected the effective proportions LULC types to explain the variation in site occupancy caused by the LULC threat category. We also included selected one-way interactions between LULC types. Transport of contaminants and sediments from disturbed landscapes to lotic systems via surface runoff can be mitigated by wetlands (Zedler and Kercher, 2005; Mitsch et al., 2015), and as such, we expected an increase of wetland LULC in the contributing watershed of a survey site to decrease the effect size of developed, agricultural crop, and herbaceous/pasture LULC on the occupancy probability of N. lewisi. We did not explore interactions between forested LULC and disturbed cover types, though riparian buffers provide a similar mitigating function as wetlands (Sweeney and Newbold, 2014; Surasinghe and Baldwin, 2015), because a variance inflation factor test revealed that forested LULC was collinear with all other types (i.e., cutoff value of four). Three one-way interactions between developed, agricultural crop, and herbaceous/pasture LULC were estimated because we expected an increase in the effective proportion of one to disproportionately increase the effect size of the others.

We chose minimum daily air temperature, total precipitation, the quadratic effects of both, and two binary covariates of survey season as covariates of detection in our analysis. We used temperature and precipitation data for the day prior to our detection/non-detection surveys because N. lewisi are believed to be largely nocturnal and captures likely occurred overnight between trap checks; hence, detection probability realized on a given day likely varied, for the most part, by weather conditions of the prior day. We expected detection probability to increase as measured air temperatures decreased and measured precipitation increased, possibly non-linearly, based on prior studies (Fedak, 1971; Braswell and Ashton, 1985; Chellman et al., 2017) and communication with NCWRC biologists. The two binary covariates of survey season were used to account for unmeasured variability across seasons.

Occupancy modeling.—We updated the knowledge of the current distribution of N. lewisi and evaluated our hypotheses using a single-season occupancy modeling framework (MacKenzie et al., 2002). We formatted the detection history data for the analysis such that each survey site had up to eight total visits during the two-year study, where visits occurred on four consecutive days each year and were recorded as $1 = N. lewisi$ detected or $0 =$ not detected. We estimated site occupancy probability ($\psi$) and daily detection probability ($p$) using the combined detection history data. We recognize that this is a potential violation of the closure assumption (MacKenzie et al., 2002); however, violating this assumption posed minimal impact in our study as we primarily detected adults, which are long-lived and maintain small home ranges (Braswell and Ashton, 1985; Beane et al., 2010).

We fit a global single-season occupancy model, containing all covariates of occupancy and detection probability (Table 2; MacKenzie et al., 2002), using the ‘unmarked’ library (Fiske and Chandler, 2011) in program R (R Core Team, 2020) and assessed its fit with a goodness-of-fit test (MacKenzie and Bailey, 2004) using the ‘AICcmodavg’ library (Mazerolle, 2020). We then explored submodels relevant to the threat categories and representing every biologically relevant combination of covariates found within the global model with a limit of $\leq 10$ terms and $\leq 1$ LULC interaction due to small sample sizes (the maximum of ten terms and one interaction was determined by fitting a range of models that had more or fewer covariates and looking at convergence and model diagnostics; we found that ten terms and one interaction was sufficient for our data). The main effect of forested LULC was not included in any submodel with other LULC types due to collinearity. Quadratic terms and interaction terms were only included in submodels with the corresponding main effects to avoid fitting uninterpretable submodels. We used $AIC_c$ (Akaikes Information Criterion corrected for small sample sizes) to identify the best fit model (Hurvich and Tsai, 1989) where
models $\leq 4.0 \Delta \text{AIC}_C$ of the top ranked model were equally supported (Burnham and Anderson, 2002). R code is provided in the supplementary materials (see Data Accessibility). We expected the top ranked model to elucidate the drivers of the current distribution of *N. lewisi*. We also expected that the estimated effect size and direction of occupancy covariates supported in the top model would allow us to infer which hypotheses were supported.

**RESULTS**

**Survey results.**—We detected *N. lewisi* ($n = 241$) at 53 sites throughout the Neuse and Tar River basins (naïve $\psi \approx 0.46$; 50 historical and three new; Fig. 1D). Eight of the 23 sites surveyed in both seasons (i.e., 35% of resurveyed sites) had different detection results between years, highlighting the challenge of confirming presence or absence at a given location. Detections occurred in the Piedmont and Coastal Plain physiographic provinces of both basins, but only in free-flowing streams with a wetted width of 10 m to 40 m. *Necturus lewisi* is known from streams $> 40$ m wide, but few sites of this size were surveyed in our study. Across all surveys, water temperature ranged 2.60°C to 18.47°C, pH ranged 6.51 to 8.44, dissolved oxygen ranged 3.46 mg/L to 12.93 mg/L, and conductivity ranged 41.50 $\mu$S/cm to 260.00 $\mu$S/cm (Table 3). Total scores from the rapid channel stability assessments performed in 2020 ranged from 7.0 to 33.5 (median = 15.5; lower scores indicate greater stability).

**Occupancy modeling results.**—The goodness-of-fit test found little evidence of overdispersion ($\hat{c} = 0.89$) in the global model. Submodels were ranked with $\text{AIC}_C$, but there was no clear top model with 22 submodels $\leq 4.0 \Delta \text{AIC}_C$ (Table 4). We created a single model-averaged model by averaging the coefficients across the top 22 submodels. Doing so allowed us to make conservative interpretations about the current drivers of occupancy. Model-averaging also allowed us to evaluate support for our hypotheses while accounting for uncertainty in the model selection process (Table 5). Using the model-averaged model, we estimated a strong negative effect of dominant substrate type ($-1.277 \pm 0.459$) on the occurrence of *N. lewisi* (Fig. 2), suggesting occupancy probability was higher in streams with coarse sediments and lower in streams with fine sediments. There was a significant, but weak ($-0.011 \pm 0.005$), negative interaction between agricultural crop and wetland LULC types in the model-averaged model, suggesting that an increase in crop or wetland LULC would increase site occupancy probability, but would decrease the effect size of the other LULC type. However, neither main effect was statistically supported because the 95% confidence intervals overlapped zero. We estimated a potentially important ($p < 0.1$) negative effect of herbaceous/pasture LULC ($-0.443 \pm 0.257$), suggesting site occupancy probability would decrease as the effective proportion of herbaceous/pasture LULC increased in the contributing watershed (Fig. 3). No detection covariates had statistical support (i.e., model-averaged confidence intervals all overlapped zero). Site-specific estimates of occupancy probability across all sites ranged from 0.003$\pm 0.019$ to 0.972$\pm 0.033$ ($\hat{\psi} = 0.495$). Daily estimates of detection probability across all sites and visits ranged from 0.418$\pm 0.061$ to 0.521$\pm 0.126$ ($\hat{p} = 0.475$).

**Hypothesis evaluation.**—We used the model-averaged results to identify which specific covariates, and in turn, which of the three primary hypotheses, had the greatest support. We found low support for the first hypothesis, that adult and juvenile mortality is caused by water quality declines. The covariates chosen to represent the pollution threat category had estimated 95% confidence intervals that overlapped zero. We found moderate support for the second hypothesis, that adult and juvenile mortality is caused by flow suppression-induced habitat alteration. One covariate (i.e., dominant substrate type) chosen to represent the flow suppression threat category was statistically supported with an estimated strong negative effect on occupancy probability. None of the other covariates in this threat category were supported in the model results. We found moderate-to-high support for the third hypothesis, that recruitment limitation is caused by sedimentation. The model results included a potentially important negative effect of herbaceous/pasture LULC and a potentially important interaction between crop and wetland LULC on occupancy probability. The effect of developed LULC was negative and forested LULC was positive, as expected, but the 95% confidence intervals overlapped zero for both, suggesting uncertainty in their estimated effects on occurrence.

**DISCUSSION**

Here we present a synthesis of the current knowledge of hypothesized threats to *N. lewisi*. We tested those hypotheses with newly collected detection/non-detection data to update the current knowledge on the species’ distribution and its drivers of occurrence. This species has quietly declined during four decades of intensive land cover conversion and water quality degradation, yet its cause of decline has remained uncertain (NCWRC, 2015). For other species,
Table 4. Results of the top submodels ($\Delta AIC_c < 4.0$) from the occupancy analysis. The covariate effects of dominant substrate type and herbaceous/pasture LULC were included in all 22 models. The interaction term of agricultural crop LULC and wetland LULC were included in 20 of 22 models. Other covariate terms estimated in the global model were less consistent among the candidate submodels. Column K shows the number of parameters included in each model. The logLik and AICc columns both show measures of model fit where higher values of log-likelihood and lower values of AICc indicate better model fit. $\Delta AIC_c$ displays the difference in fit among candidate models where 0 represents the best fit.

<table>
<thead>
<tr>
<th>Detection ($p$)</th>
<th>Occupancy ($\phi$)</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>$\Delta AIC_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>p() psi(Substrate + Pasture + Developed + Crop*Wetland + Channel Stage + Channel Stage²)</td>
<td>10</td>
<td>-234.664</td>
<td>491.4</td>
<td>0</td>
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<tr>
<td>p(Season) psi(Substrate + Pasture + Developed + Crop*Wetland)</td>
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<td>1.183</td>
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<tr>
<td>p() psi(Substrate + Pasture + Crop*Wetland + NPDES + Channel Stage + Channel Stage²)</td>
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<td>p(Season) psi(Substrate + Pasture + Crop*Wetland + NPDES)</td>
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<tr>
<td>p() psi(Substrate + Pasture + Crop*Wetland + Channel Stage + Channel Stage²)</td>
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<td>-236.623</td>
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<td>p(Season) psi(Substrate + Pasture + Crop*Wetland)</td>
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<td>-236.664</td>
<td>493.0</td>
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<tr>
<td>p() psi(Substrate + Crop + Developed + Pasture*Wetland + NPDES + Upstream Dam)</td>
<td>10</td>
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<td>493.3</td>
<td>2.132</td>
<td></td>
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<tr>
<td>p(Season) psi(Substrate + Pasture + Forest + Crop*Wetland)</td>
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<td>2.537</td>
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<tr>
<td>p(Precip.) psi(Substrate + Pasture + Crop*Wetland + Channel Stage + Channel Stage²)</td>
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<td>-236.122</td>
<td>494.3</td>
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<tr>
<td>p(Season) psi(Substrate + Pasture + Crop*Wetland + Benthic)</td>
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<td>494.5</td>
<td>3.089</td>
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<td>3.454</td>
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<td>3.477</td>
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<td>p(Precip. + Precip.²) psi(Substrate + Pasture + Developed + Crop*Wetland)</td>
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<td>495.0</td>
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<td>p(Precip. + Precip.²) psi(Substrate + Pasture + Crop*Wetland + NPDES)</td>
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<td>3.621</td>
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<tr>
<td>p() psi(Substrate + Pasture + Crop*Wetland + Channel Stage + Channel Stage² + Upstream Dam)</td>
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<td>-236.478</td>
<td>495.1</td>
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<tr>
<td>p(Min. air temp.) psi(Substrate + Pasture + Crop*Wetland + Channel Stage + Channel Stage²)</td>
<td>10</td>
<td>-236.594</td>
<td>495.3</td>
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<td>p() psi(Substrate + Pasture + Crop*Wetland + Benthic + Channel Stage + Channel Stage²)</td>
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<td>495.3</td>
<td>3.901</td>
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<td>p(Season) psi(Substrate + Pasture + Crop*Wetland + Downstream Dam)</td>
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<td>495.4</td>
<td>3.969</td>
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<td>p(Season) psi(Substrate + Pasture + Crop*Wetland + Channel Stage)</td>
<td>10</td>
<td>-236.666</td>
<td>495.4</td>
<td>3.992</td>
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uncertainty has led to vague and ineffective recovery criteria in plans, and a difficulty in implementing actions and assessing the status of recovery over time (Lawler et al., 2002; Doak et al., 2015; Troyer and Gerber, 2015). This study aimed to minimize threat uncertainty for *N. lewisi* early in the recovery planning and implementation process by evaluating potential threats through a comprehensive information synthesis and occupancy modeling approach. We focused only on the broad threats of pollution, flow suppression, and LULC for this analysis and hypothesized they would result in 1) adult and juvenile mortality caused by water quality declines, 2) adult and juvenile mortality caused by habitat alterations, and 3) recruitment limitation caused by sedimentation of nesting habitat, respectively.

We examined a range of possible drivers of occurrence, representing all broad threat categories; however, only a few effects were supported. The strong negative effect of fine sediments on occupancy of *N. lewisi* found in this study was supported in prior work by Braswell and Ashton where they speculated that silted stream segments may be unsuitable.

**Fig. 2.** Estimated occupancy probability of *N. lewisi* across four categories of substrate type using the coefficient estimate of dominant substrate from the model-averaged model. 0 = Cobble, 1 = Gravel, 2 = Sand, and 3 = Silt. Estimated occupancy probability declines as the dominant substrate type at the survey site becomes finer.

**Fig. 3.** Estimated occupancy probability of *N. lewisi* using the coefficient estimate of effective herbaceous/pasture LULC from the model-averaged model. Occupancy probability decreases precipitously as the effective proportion of herbaceous/pasture LULC increases within the watershed of the survey site.

**Table 5.** Model-averaged model results (top 22 submodels ≤ 4.0 ΔAICc). Dominant substrate type (included in the Flow Suppression Threat Category) and the interactive effect of Crop LULC and Wetland LULC (included in the Land Use/Land Cover Threat Category) were the only effects supported (model-averaged 95% CIs did not overlap zero). The effect of herbaceous/pasture LULC (included in the Land Use/Land Cover Threat Category) was potentially important (*P* < 0.1).

<table>
<thead>
<tr>
<th>Threat Category: Pollution</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
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<tr>
<td>NPDES</td>
<td>-2.5570</td>
<td>4.9980</td>
<td>-12.3531</td>
<td>7.2391</td>
</tr>
<tr>
<td>DEQ Benthic Score</td>
<td>0.0278</td>
<td>0.1514</td>
<td>-0.2689</td>
<td>0.3246</td>
</tr>
<tr>
<td>Threat Category: Flow Suppression</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist. to upstream dam</td>
<td>-0.0268</td>
<td>0.0761</td>
<td>-0.1760</td>
<td>0.1225</td>
</tr>
<tr>
<td>Dist. to downstream dam</td>
<td>0.0016</td>
<td>0.0188</td>
<td>-0.0352</td>
<td>0.0384</td>
</tr>
<tr>
<td>Substrate</td>
<td>-1.2770</td>
<td>0.4593</td>
<td>-2.1772</td>
<td>-0.3768</td>
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<tr>
<td>Channel Stage</td>
<td>1.1040</td>
<td>1.3090</td>
<td>-1.4616</td>
<td>3.6696</td>
</tr>
<tr>
<td>(Channel Stage)^2</td>
<td>-0.1860</td>
<td>0.2196</td>
<td>-0.6164</td>
<td>0.2444</td>
</tr>
<tr>
<td>Threat Category: Land Use/Land Cover</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Developed LULC</td>
<td>-0.0197</td>
<td>0.0321</td>
<td>-0.0825</td>
<td>0.0432</td>
</tr>
<tr>
<td>Forested LULC</td>
<td>0.0038</td>
<td>0.0136</td>
<td>-0.0228</td>
<td>0.0303</td>
</tr>
<tr>
<td>Crop LULC</td>
<td>0.1713</td>
<td>0.1111</td>
<td>-0.0465</td>
<td>0.3891</td>
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<tr>
<td>Herbaceous/Pasture LULC</td>
<td>-0.4427</td>
<td>0.2566</td>
<td>-0.9456</td>
<td>0.0602</td>
</tr>
<tr>
<td>Wetland LULC</td>
<td>0.1002</td>
<td>0.0703</td>
<td>-0.0375</td>
<td>0.2379</td>
</tr>
<tr>
<td>Crop*Wetland</td>
<td>-0.0108</td>
<td>0.0050</td>
<td>-0.0206</td>
<td>-0.0010</td>
</tr>
<tr>
<td>Pasture*Wetland</td>
<td>0.0018</td>
<td>0.0065</td>
<td>-0.0109</td>
<td>0.0145</td>
</tr>
</tbody>
</table>
for *N. lewisi*, but they noted most sites had very little silt or sedimentation at the time of their study (Braswell and Ashton, 1985). A more recent distribution study of *N. alabamensis*, a federally protected and ecologically similar congener to *N. lewisi*, reported site absence associated with substrates covered in fine silt, possibly because silt cover could have reduced the prey community, reduced nesting sites, and reduced individual respiration potential (Durflinger Moreno et al., 2006).

Pasture near streams is known to contribute to stream sedimentation (Owens et al., 1996; Byers et al., 2005), which supported our interpretation of the modeled effects of dominant substrate type and herbaceous/pasture LULC on occupancy of *N. lewisi*. While the effect of herbaceous/pasture LULC was not statistically significant in the model-averaged results, it was significant in many of the candidate submodels, and we expect that more data would strengthen this signal. One 2014 study analyzing stream salamander abundance and species richness as a function of historical land use practices in North Carolina, South Carolina, and Georgia found that assemblages were negatively impacted in streams historically dominated by agriculture and the negative effects of erosion and sedimentation were greatest in the Piedmont physiographic region (Surasinghe and Baldwin, 2014), matching our observations and results. Lastly, we estimated a significant negative interaction between crop and wetland LULC. This relationship seemed reasonable but was complicated by the counterintuitive estimated positive effect of crop LULC. The estimated positive effect of crop LULC likely resulted from the ubiquity of agricultural crops in the Coastal Plain, where naïve site occurrence of *N. lewisi* was also high. The implication of the interactive effect of crop and wetland LULC on occupancy is unclear.

While substrate composition and certain LULC types may describe range-wide occurrence patterns, other factors that we have not attempted to measure or model may influence occurrence at smaller regional scales. For example, sites in the upper Tar River of Granville County were historically occupied (Braswell and Ashton, 1985), but *N. lewisi* went undetected during our surveys (however, presence has since been confirmed at one site during a 2023 resurvey; E. W. Teitsworth, unpubl. data). We observed coarse substrates indicative of habitat suitability at many of these sites, making the reason for apparent absences unclear. A USFWS biologist reported in the SSA that this portion of the Tar River dried almost entirely during drought conditions in 2007–2008 (USFWS, 2017). Local populations were likely extirpated from much of this region during that drought event and were unable to recolonize due to the presence of a relict mill dam downstream. These sites were not omitted as outliers in the analysis because this alternative cause of absence could not be confirmed. Region-specific stressors have historically contributed to declines in occurrence of *N. lewisi* (e.g., NaOH spill in Wake Co.; Braswell and Ashton, 1985) and pose continuing challenges to estimating range-wide occupancy with fine resolution.

We expected to find a negative effect of developed LULC on the occupancy probability of *N. lewisi* as it has been implicated in the declines of both aquatic (Wineland et al., 2019) and semi-aquatic (Price et al., 2011) salamanders and because the most dramatic declines in observed occurrence have been in the rapidly urbanizing Piedmont region of the Neuse River basin. This portion of the basin drains the City of Raleigh and most of the City of Durham, with a combined population of approximately 745,000, roughly triple the size as during the NCMNS surveys when the species was commonly encountered there. The lack of support for an effect of developed LULC on occupancy may have been a result of low survey effort in urban-dominated landscapes during our two years of data collection. It may also be possible that developed LULC affects other vital rates, such as survival, which would take decades of declining abundance to present as a decline in occurrence for this long-lived species. Future targeted surveys in the Raleigh-Durham metropolitan area would help explain the mechanism behind urbanization and the apparent decline of *N. lewisi*.

The lack of support for detection probability covariates suggests that, although detection probabilities were highly variable, we did not find suitable covariates to explain this variation. Air temperature had a demonstrated relationship with detectability in a prior study (Braswell and Ashton, 1985), but had no effect in this analysis, likely because it did not vary as much within our survey period (late November–early March) as in the Braswell and Ashton study (October–May). We eliminated October, April, and May from our surveys because sustained higher air temperatures (e.g., > 18°C) generally do not yield detections with minnow trapping surveys (Braswell and Ashton, 1985; E. W. Teitsworth, unpubl. data). Although total precipitation was not supported as a proxy of flow conditions in the model, it is plausible that flow conditions may influence detection probability. Periods of high river flow were associated with high capture success in a recent study with a congener, *N. maculosus* (Chellman et al., 2017). Personal observations in this study and communication with NCWRC biologists suggest large variations in water volume may stimulate or hinder movement of *N. lewisi* and thus detection probability. Future studies should explore the relationship between water discharge patterns and detection probability.

We evaluated support for our hypotheses that were formed during threat synthesis by assuming that their effects to vitals rates could be estimated through realized changes in occupancy. This assumption facilitated the exploration of the mechanisms driving occurrence using limited detection/non-detection data. We found little support for our first hypothesis, that occurrence declines were the result of adult and juvenile mortality caused by the pollution threat category. This suggested that the threat of pollution, as measured by our metrics, was not a primary driver of occupancy. However, occupancy is only a rough proxy for survival probability, which we could not directly estimate with our data. Moreover, our survey methods were biased towards adult detections, thus reducing the ability to make inferences about the impacts of pollution on juvenile or egg mortality, growth rates, or other vital rates that could negatively affect populations of *N. lewisi*. Additional demographic data and more precise covariate information are needed to adequately evaluate the pollution category as a threat to species persistence.

We found moderate support for the second hypothesis, that occurrence declines were the result of adult and juvenile mortality caused by the flow suppression threat category. Prior work (Braswell and Ashton, 1985; NCWRC, 2015) and results from our surveys suggest that flow suppression does reduce local occurrence in impounded stream reaches, but the modeled results indicated that this effect
likely does not extend far upstream or downstream. This
suggested that the threat of flow suppression was not a pri-
mary driver of occupancy, apart from its contribution to
sedimentation. Again, occupancy was only a rough proxy
for survival probability in response to flow suppression,
which limited our full interpretations of population
responses to the threat category.

Our evaluation yielded the highest support for our third
hypothesis, that occurrence declines were the result of
recruitment limitation caused by LULC-induced sedi-
mentation of nesting habitat. If we had placed the dominant
substrate type covariate in the LULC threat category a priori,
which is logical given the relationship between landscape
disturbance and sedimentation (Owens et al., 2005; Wol-
man and Schick, 1967), the LULC threat category
would have contained all significant ($P < 0.05$) and nearly signifi-
 cant ($P < 0.1$) covariates found in the model-averaged
model. Support for this hypothesis was unsurprising given
our understanding of the species’ underlying biology and
prior work with similar species. In suitable habitats, females
deposit eggs on the underside of flat rocks, woody debris, or
other protective structures along the streambed in early
spring (Ashton and Braswell, 1979). Research in Wisconsin
(Casper, 1998) and Indiana (Minton, 1998) determined sedi-
mentation could limit survival of eggs and larvae of the
Common Mudpuppy (N. maculosus) as interstitial spaces in
the streambed were filled. Populations of the ecologically
comparable Hellbender (Cryptobranchus alleganiensis) also
respond negatively to stream sedimentation as it decreases
nesting site availability (Bodinof Jachowski and Hopkins,
2018) and larval habitat (Unger et al., 2021). Under these
conditions, adult Hellbenders have been found to persist in
a functionally non-reproductive state for decades before the
population is extirpated (Bodinof Jachowski and Hopkins,
2018). This situation is often referred to as an “extension
debt,” where the habitat becomes unsuitable for meeting
the species’ needs, but a population response may go long
undetected because of species-specific life history strategies,
such as being long-lived (Tilman et al., 1994; Kuussaari
 et al., 2009). Extinction debt has been suggested as a pri-
mary driver of decline for many amphibian species (Sem-
litsch et al., 2017), and we suspect LULC-induced stream
sedimentation is creating this phenomenon for N. lewisi.

Data-limited species like the Neuse River Waterdog create
challenges for conservation because threats to their persis-
tence are not well understood. Yet threat evaluation is a ne-
cessary first step in preparing for and implementing species
recovery (Clark et al., 2002; Lawler et al., 2002). To achieve
threat evaluation with a paucity of data, we leveraged our
synthesized knowledge base to generate hypotheses of how
populations might respond to identified threats (USFWS,
2017) and then evaluated those threats and hypotheses in
an occupancy modeling approach (MacKenzie et al., 2002).
The results suggested that while multiple threats may be
driving occurrence (potentially at different scales), the
threat of intensive land uses within the species’ range poses
the greatest present threat to occurrence. Land use practices
that decrease stormwater infiltration and increase surface
erosion, such as livestock pastures and urban development,
significantly modify the hydrological and geomorphologi-
cal stream processes that control channel stability and sub-
strate composition (Russell et al., 2017). The modification
of these forces generally leads to a homogenization and
sedimentation of instream habitat and benthic substrates
(Roy et al., 2016), which are believed to limit reproductive
opportunities for benthic-nesting aquatic salamanders
(Durlinger Moreno et al., 2006; Bodinof Jachowski and
Hopkins, 2018). Our analysis supported the hypothesis that
observed declines in the occurrence of N. lewisi are a delayed
result of sedimentation-induced recruitment limitation.
This study builds on the work of prior survey efforts (Bra-
well and Ashton, 1985; NCWRC, 2015) and emphasizes that
continued long-term monitoring would facilitate the direct
evaluation of landscape change on the species’ population
dynamics. Future studies that evaluate landscape change and
its expected contribution to sedimentation-induced recruit-
ment limitation will be crucial for guiding future recovery
actions and defining measurable recovery metrics for this
protected and narrowly endemic aquatic species.

DATA ACCESSIBILITY

Supplemental material is available from the GitHub Reposi-
tory: https://github.com/ericteitsworth/Capital-to-Coast_N.-lewisi. Unless an alternative copyright or statement
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Service. This study was approved by the North Carolina State
University Institutional Animal Care and Use Committee
Protocol #18-151-0, followed the ASIH Guidelines for Live
Amphibians and Reptiles in Field and Laboratory Research,
and was performed under the North Carolina Wildlife Resources
Commission Endangered Species Permit #ES00628 and North
Carolina Division of Parks and Recreation Scientific Research
and Collecting Permit #0464.

LITERATURE CITED

Ashton, R. E., Jr. 1985. Field and laboratory observations
on microhabitat selection, movements, and home range


Mazerolle, M. J. 2020. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.3.2. https://cran.r-project.org/package=AICcmodavg


