

FACTORS INFLUENCING DISTRIBUTION OF THE EASTERN HELLBENDER IN THE
NORTHERN SEGMENT OF ITS RANGE

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ABSTRACT

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Eastern Hellbender populations are experiencing drastic, range-wide declines. Conservation strategies to address these trends are needed, but the factors underlying population occurrence within stream networks are poorly known. I compared habitat elements across historically occupied and apparently unoccupied sites throughout the Upper Susquehanna sub-basin of New York State. Historically occupied sites contained larger rocks and less soft sediment than unoccupied sites. I also used predictive models used to examine the species' distribution in Pennsylvania, which indicated that specific geologic features (i.e. rock and surficial material types) are the strongest predictors of Eastern Hellbender occurrence. My research suggests that Eastern Hellbender occurrence is dependent on isolated geological features, low levels of sedimentation, moderate elevations and extensive forest cover; these habitat requirements have caused the species to be vulnerable to extirpation in its northern range segment.

Key Words: Eastern Hellbender (*Cryptobranchus alleganiensis*), MaxEnt, predictive modeling, Salamander conservation, habitat characterization, Geographic Information System (GIS)

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INTRODUCTION

The Eastern Hellbender (*Cryptobranchus a. alleganiensis* Daudin) is a fully aquatic salamander that occupies streams and rivers from southern New York State to northern Alabama and west into Missouri. The genus *Cryptobranchus* is divided among two sub-species: the Eastern Hellbender, which occurs in the Susquehanna and Ohio drainages, and the Ozark Hellbender (*C. a. bishopi*), restricted to southeastern Missouri and a small section of adjacent Arkansas (Peterson et al., 1988). These are members of Family Cryptobranchidae, which includes just two other species: the Chinese Giant Salamander (*Andrias davidianus*) and the Japanese Giant Salamander (*Andrias japonicus*). Despite being the smallest members of Family Cryptobranchidae the Eastern Hellbender is still the largest salamander in the New World with a record total length of nearly 74 cm (Petranka, 1998) and a mass that can exceed 2 kg.

Fertilization in this species is external. This reproductive trait is unique among North American salamanders (although reproduction has not yet been observed in Family Sirenidae and is inferred to also be external). Phylogenetic analysis of ribosomal RNA sequences (Larson, 1991; Larson and Dimmick, 1993; Weins et al., 2005) and morphological characters (Sever 1991a, b) indicate that Cryptobranchidae is closely related to the externally fertilizing Asiatic Family Hynobiidae, together forming the suborder Cryptobranchoidea.

These salamanders use large, flat rocks for cover (Hillis and Bellis, 1971; Noeske and Nickerson, 1979; Soule and Lindberg, 1994), typically remaining under their rocks throughout the day and wandering the stream bottom by night (Noeske and Nickerson, 1979; Swanson, 1948; Humphries and Pauley, 2000). The species exhibits negative phototaxis (Reese, 1906; Smith, 1907; Pearse, 1910) and flat rocks may permit less light penetration under the rock margins compared to rounded rocks (Nickerson et al., 2003). Eastern Hellbenders defend cover

rocks against intrusion by other Eastern Hellbenders (Hillis and Bellis, 1971) and rocks are rarely occupied by more than one individual (Smith, 1907). Crayfish are the principal food source and can comprise 80-100% of an Eastern Hellbender's diet (Netting, 1929; Swanson, 1948; Peterson et al., 1989). The species will also eat fish, worms, and other invertebrates (Bishop, 1948).

Eastern Hellbender populations range-wide are declining in both local abundance and occupied range extent (Gates et al., 1984; Trauth et al., 1992; Wheeler et al., 2003; Phillips and Humphries, 2005). Population declines first reported by Smith (1948) appear to have accelerated in the latter half of the 20th century. Habitat destruction is considered the single greatest threat to Eastern Hellbenders range-wide (Mayasich and Phillips, 2003) due to the species' sensitivity to changes in stream conditions, particularly sedimentation (Nickerson et al., 2003) and hydrology (Routman, 1993; Jensen, 1999). Stream hydrology, substrate composition, and water temperature can be drastically altered by human activities (Routman, 1993; Jensen, 1999). The primary mode of Eastern Hellbender habitat destruction is stream sedimentation in which silt and other soft sediments fill the narrow spaces under rocks that Eastern Hellbenders rely on for cover (Gates et al., 1985; Nickerson and Tohulka, 1986; Wheeler et al., 2003). The amphibian fungal disease chytridiomycosis may also be associated with declines of some populations in Pennsylvania (Peter Petokas, unpubl. data) and Missouri (Jeffrey Briggler, pers. comm.). Other range-wide threats to the Eastern Hellbender include illegal collection for the pet trade and research purposes, and pollution (Mayasich and Phillips, 2003).

Factors underlying population occurrence within stream networks are poorly known (Hillis and Bellis, 1971; Gates et al., 1985; Nickerson et al., 2003). Correlations have been made

between population abundance and local habitat elements within and among occupied sites (Hillis and Bellis, 1971; Nickerson et al., 2002; Nickerson et al., 2003) but there have been no studies to date contrasting habitat components of occupied and apparently unoccupied sites. Furthermore, current understanding of Eastern Hellbender ecology is based on small-scale, local studies—investigation into the contribution of broad-scale environmental variables (e.g. bedrock morphology) to population occurrence is completely lacking. Several recent studies have emphasized the importance of examining regional influences on riparian systems, indicating that stream conditions can be affected by the composition and configuration of landscape features outside the riparian corridor (Gergel et al., 2002; Allan, 2004; Gergel, 2005; Kearns et al., 2005). For example, in a study at the Santa Clara Basin, California, Kearns et al. (2005) found that two factors—the quantity and distribution of land use types throughout the watershed—explained 85% of the variation in water quality.

The rapid range-wide decline of Eastern Hellbender populations warrants a more in-depth understanding of the factors underlying the species' distribution. To meet this goal, I examined local and regional environmental elements relating to population occurrence in New York State and Pennsylvania. The objectives of the first chapter were to determine current Eastern Hellbender distribution in the Upper Susquehanna sub-basin of New York State and compare habitat features across historically occupied and apparently unoccupied locations. The second chapter is an investigation of Eastern Hellbender occurrence throughout the species' northern range segment in which I used a predictive modeling algorithm to quantify the importance of broad-scale environmental variables to population occurrence.

CHAPTER 1: Habitat Elements Associated with Eastern Hellbender Occurrence in the Upper Susquehanna River Sub-basin of New York State

Introduction

Eastern Hellbender populations are experiencing drastic range-wide declines – the New York State population segment is no exception (Gates et al., 1984; Trauth et al., 1992; Phillips and Humphries, 2005; Wheeler et al., 2003). Within New York State Eastern Hellbenders occur in the Susquehanna River and Allegheny River drainages. Historic records (Bishop, 1941; NYSDEC, 2006) indicate that Eastern Hellbender occurrence in the Susquehanna River watershed within New York State is restricted to the Upper Susquehanna sub-basin. The species is listed as a “species of greatest conservation need” for both the Susquehanna River and Allegheny watersheds (NYSDEC, 2006). Eastern Hellbenders have been listed as a species of Special Concern in New York State since 1983 (Bothner and Gottlieb, 1991) but have no federal protection status.

Eastern Hellbender populations are typically found in the riffle and run sections of cool water streams, tending to be absent from pool areas (Hillis and Bellis, 1971; Nickerson et al., 2003). These salamanders absorb dissolved oxygen through their highly folded skin and their microhabitat preference may be associated with a limited gas exchange capability (Ultsch and Duke, 1990). Moreover, cooler water holds more dissolved oxygen and some research has suggested that Eastern Hellbenders do not readily acclimate thermally (Hutchison et al., 1973). Mayasich and Phillips (2003) suggest that climate change and removal of forest cover overhanging streams may be degrading Eastern Hellbender habitat by increasing water temperatures; other researchers have speculated that warming air and water temperatures are contributing to Eastern Hellbender declines (Dodd, 1997; Pounds, 2001). Acidic conditions

caused by near-stream construction (Huckabee et al., 1975) or mining (Peter Petokas, unpubl. data) may also be associated with population losses; Nickerson et al. (2003) observed fewer Eastern Hellbenders in a slightly acidic stream than in a more alkaline stream nearby.

Despite the species' wide range, local distribution is patchy and factors underlying population occurrence within stream networks remain poorly known (Hillis and Bellis, 1971; Gates et al., 1985; Nickerson et al., 2003). Correlations have been made between population abundance and local habitat elements (e.g. average rock size) within and among occupied sites (Hillis and Bellis, 1971; Nickerson et al., 2002; Nickerson et al., 2003), but there have been no studies to date contrasting habitat components of occupied and apparently unoccupied sites. It is necessary to determine not only why populations occur in some areas, but also why they do not occur in others. Such comparisons will further expand understanding of what habitat features are essential to population persistence and help guide proposed reintroduction programs for restoring Eastern Hellbenders to parts of their historic range. To this end, I compared 10 habitat elements within historically occupied and apparently unoccupied sites (henceforth referred to as "non-historic" sites) and stream segments of the Upper Susquehanna sub-basin of New York State. My objectives were to (1) determine whether Eastern Hellbenders were still present at historically occupied sites, (2) search for previously unreported populations within the sub-basin, and (3) assess the influence of local habitat elements on current and historical patterns of Eastern Hellbender occurrence.

Methods

Study area

The Susquehanna River watershed drains large portions of New York State, Pennsylvania, and Maryland before emptying into Chesapeake Bay and is the second largest watershed east of the

Mississippi, exceeded in size only by the Ohio River basin. The Upper Susquehanna sub-basin covers approximately 12,055 km² and falls mostly within New York State with less than 10% of the drainage area in Pennsylvania (Susquehanna River Basin Commission) (Fig. 1).

Nearly all of the Upper Susquehanna sub-basin occurs within US Level III Ecoregion 60- the Northern Appalachian Plateau and Uplands (Wood, 1996) and is characterized by low hills and broad valleys. Major land use throughout the sub-basin is a mixture of two-thirds forest and one-third farmland (Boyer et al., 2002). The gentle topography of the region coupled with productive till soils deposited by Wisconsinan Age glaciers has led to extensive agricultural development.

Sampling site selection

Information on historic Eastern Hellbender distribution in the Upper Susquehanna sub-basin was obtained from the New York Natural Heritage Program (NHP) Database (NYSDEC, 2006). Twenty-two historic population sites are described in the NHP Database, which was compiled from previous population surveys in New York State dating back to 1923. Because of the fragile status of Eastern Hellbenders in the Upper Susquehanna sub-basin all site location data used in this study are archived with the New York NHP.

ArcMap 9.2 (ESRI Redlands, CA) was used to develop the sampling frame for surveying for unknown but possibly extant Eastern Hellbender populations. To create the sampling frame I intersected a stream hydrography layer with a road layer to identify all of the bridges within the Upper Susquehanna sub-basin. Bridge sites were used to allow for rapid access to streams without crossing private land and because most recorded Eastern Hellbender population sites occurred near bridges (NYSDEC, 2006). Potential bias of sampling at bridges was assessed by

comparing road density around bridge sites to an equal number of randomly selected stream sites.

Once bridges were identified the sampling frame was further stratified using a ranking system based on habitat features known to be associated with population occurrence. Sampling sites were divided among four classes: (1) “historic sites,” (2) “high priority” sites, (3) “medium priority” sites, and (4) “random sites.” “Priority” criteria were based on interactions between Strahler stream order and the presence of adjacent forest cover. The presence of a forested riparian buffer is reportedly a strong indicator of Eastern Hellbender habitat quality (Smith and Minton, 1957; Williams et al., 1981; Mayasich and Phillips, 2003) and populations cannot persist in small or ephemeral streams. As such, “high priority” sites were considered those bordered by forest and occurring in third or fourth order streams or in streams that historically supported Eastern Hellbender populations. “Medium priority” sites were considered to be those that occurred in the same streams as “high priority” sites but lacked adjacent forest cover. Criteria were levied by buffering the hydrography layer by 30 m and identifying intersections with the forested components of the National Land Cover Dataset (NLCD) 2001 at 30 m resolution (Homer et al., 2004) (Table 1). I selected 20 “high priority” sites, 10 “medium priority” sites, and eight “random” sites. “Random sites” were selected entirely at random with no preset habitat requisites. The final survey sample was 59 because one “high priority” and one random site could not be visited due to logistical constraints and one historic site was later divided into two to permit complete survey coverage.

Survey units and data collection

Survey units were variable width stream sections 100 m in length. Sampling within a site was performed at riffle and run sections of stream, as these are hydrologic features known to be associated with Eastern Hellbender presence (Hillis and Bellis, 1971; Nickerson et al., 2003; Foster et al., 2008). We surveyed each unit for Eastern Hellbenders using the rock lifting technique—considered to be among the most effective and least habitat destructive search techniques available (Peterson, 1987; Soule and Lindberg, 1994). One searcher gently lifted all moveable rocks > 15 cm in minimal axis diameter while another felt beneath for Eastern Hellbenders until up to 100 rocks had been lifted. Tactile inspection was used because water clarity was generally poor and it required that rocks be lifted only a few centimeters reducing disturbance to the delicate silt layer on and beneath rocks.

Searches for larval Eastern Hellbenders were conducted using three sampling techniques at 10 sites that based on habitat features (Nickerson and Tohulka, 1986; Nickerson et al., 2003) were considered promising for supporting larvae. Bank searches were performed by hand for 15 minutes in 10 plots (1 m wide by 2 m long) randomly selected based on position within the 100 m site. Three 1 m by 3 m plots were then seine-netted by one searcher removing large rocks from the plot and then gently stirring the substrate with their hands while another searcher held the seine net downstream. Seine net plots were selected based on the type of substrate: areas free of soft sediment and containing cobble to gravel size rocks were preferred. Last, four to eight litterbags constructed from 1.9 cm aperture plastic deer fencing were deployed at the 10 selected sites throughout July and August of 2008 and checked monthly until late October 2008 and again beginning in May 2009. The bags were stuffed with a variety

of materials taken from the stream and included gravel, cobble sized rocks, leaf litter, and mixtures of each to determine if potential colonists preferred a particular material composition.

Habitat covariates

Ten habitat variables were measured at each site (Table 2). Given the reported importance of streamside forest to Eastern Hellbender habitat quality (Smith and Minton, 1957; Williams et al., 1981) percent forest canopy cover measurements were taken every 5 m using a densiometer on both shores then averaged for each site. We also recorded the minimum diameter of each rock lifted to the nearest cm. Stream substrate condition was characterized by recording the presence of soft sediment > 3 cm deep at 1 m intervals to determine percent of embedded substrate (that is, “embeddedness”).

We assessed crayfish relative abundance by recording the presence of crayfish under the rocks lifted while searching for Eastern Hellbenders because (1) crayfish abundance may serve to limit Eastern Hellbender population size (Netting, 1929; Peterson et al., 1989), and (2) the Upper Susquehanna sub-basin is host to the exotic Rusty Crayfish (*Orconectes rusticus* Girard), native to the Ohio River drainage and known for its aggressive interactions with other species (Hobbs, 1989; Larson, 2009). Last, temperature, pH, and conductivity were measured at each site in July, August, and September in 2008 and again in 2009 using a multi-probe meter (YSI 556, YSI Inc., Yellow Spring, OH). Thermal profiles of sites were determined with pre-calibrated temperature data-loggers (Thermochron iButtons, Dallas Semiconductor, Dallas, TX) deployed under large rocks at each site to record hourly temperature starting July 2008 and retrieved after two months.

Contrasts of habitat features between sites and stream systems were made using Student's independent sample *t*-tests (Sokal and Rohlf, 1995). Prior to analysis, proportional data were transformed by taking the arcsine of the variable's square root value (Sokal and Rohlf, 1995). Statistical differences associated with $\alpha \leq 0.05$ were considered statistically significant. All means are reported ± 1 SD (n).

Results

Current Eastern Hellbender distribution

Two Eastern Hellbenders were located during the course of the study. The first was found at a historic site thought extirpated since 2000; the second was at a previously undocumented "high priority" site. The individual at the "high priority" site was beneath a concrete bank reinforcement "riprap" slab on a bridge abutment. Both were mature females in apparent good health. No larvae were found using any of the three sampling techniques, but litterbags at four of the 10 sites were colonized by adult Two-Lined Salamanders (*Eurycea bislineata*) when checked in August of 2008.

Sampling frame evaluation

Although "medium priority" sites were identified as lacking forest cover in the GIS model, the proportion of shoreline cover did not vary between "high priority" sites (0.38 ± 0.19 (19)) and "medium priority" sites (0.31 ± 0.17 (10)), ($P = 0.38$, effect size = 22.0%). Moreover, shoreline cover did not have the expected moderating effect on water temperature or temperature fluctuation at sampling sites. Mean water temperature at "medium priority" sites ($21.12^{\circ}\text{C} \pm 0.37$ (10)), which had less forest cover, did not differ from that at "high priority"

sites ($20.98^{\circ}\text{C} \pm 0.90$ (19)), ($P = 0.81$, effect size = 0.63%). Temperature range was also not different ($P = 0.24$, effect size = 22.31%) (Table 3).

Road density was higher near bridge-centered sampling sites (4.73 km/km^2) than around sites selected from random stream points (1.84 km/km^2), ($P < 0.001$, effect size = 156.52%) (Table 4). Road density was greatest, however, around historic population sites (5.28 km/km^2), and did not differ from bridge sites ($P = 0.58$, effect size = 11.59%). While these values are atypical for the Upper Susquehanna sub-basin as a whole (1.22 km/km^2), road density did increase nearer to streams: $< 1 \text{ km}$ from streams road density was 1.55 km/km^2 , compared to 1.40 km/km^2 1 to 3 km from streams.

Habitat covariates

Three of the 10 habitat variables examined differed between historic and non-historic sites: minimum rock diameter, “embeddedness,” and conductivity. Historic sites contained larger rocks ($42.43 \text{ cm} \pm 14.38$ (23)) than non-historic sites ($29.11 \text{ cm} \pm 15.19$ (36)), ($P < 0.01$, effect size = 45.76 %), and were less “embedded” (0.13 ± 0.24 (23)) than non-historic sites (0.31 ± 0.29 (36)), ($P < 0.01$, effect size = 57.01 %) (Table 5). Average rock size at the occupied historic site was 58.68 cm—the largest recorded—and was 51.00 cm at the site where the second Eastern Hellbender was located, a value atypically large for non-historic sites.

Conductivity was lower in historic sites ($261.99 \mu\text{S} \pm 58.34$ (23)) than in non-historic sites ($297.46 \mu\text{S} \pm 58.34$ (36)), ($P < 0.05$, effect size = 11.92 %). Conductivity was also the only habitat variable to differ between historic streams ($272.10 \mu\text{S} \pm 59.46$ (23)) and non-historic streams ($325.67 \mu\text{S} \pm 44.43$ (36)), varying more so than between historic and non-historic sites ($P < 0.01$, effect size = 16.45 %). The other water quality variables examined were similar

across historic and non-historic sites. Temperature range was smaller at historic sites (22.38°C compared to 23.65°C), while the average temperature at historic sites (21.68°C) was slightly higher than in non-historic sites (21.02°C). Average pH at historic and non-historic sites varied by less than 1% (Table 5).

The relative frequency of crayfish was similar throughout the sampling area (0.34 ± 0.23 (23) at historic sites; 0.26 ± 0.21 (36) at non-historic sites). The Rusty Crayfish was the most abundant species at all sites and was only absent from one site, which did not support any crayfish. In contrast to the cosmopolitan distribution of the Rusty Crayfish, the relative frequency of native crayfish was much lower throughout the sub-basin: 0.03 ± 0.13 (23) at historic sites and 0.05 ± 0.17 (36) at non-historic sites (Table 5).

Discussion

Detection of only two Eastern Hellbenders despite extensive sampling in 2008 is a strong indication of the species' decline in the Upper Susquehanna sub-basin. However, accounts in the New York Natural Heritage Program Database suggest that Eastern Hellbenders may have always been comparatively less abundant in the Upper Susquehanna sub-basin than in other segments of their range (NYSDEC, 2006). For example, researchers in other regions have found recent demographic shifts toward higher proportions of mature individuals (Wheeler et al., 2003) while gilled larvae have never been reported in the Upper Susquehanna sub-basin and nests have been discovered at only four locations (NYSDEC, 2006).

An abundance of large, flat rocks is a consistent requirement to support Eastern Hellbenders (Hillis and Bellis, 1971; Noeske and Nickerson, 1979; Soule and Lindberg, 1994) and I found that historically occupied sites did have larger rocks. While the size of rocks in

streams is relatively stable over time, rocks can be buried by sediment and rendered useless to Eastern Hellbenders. Excess sediment load in streams has been blamed for the extirpation of many Eastern Hellbenders populations (Hillis and Bellis, 1971; Gates et al., 1985; Nickerson and Tohulka, 1986; Wheeler et al., 2003). Routman (1993) speculated that colonization of new habitat will only occur when streams have low silt loads. It is also important to note that substrate conditions in streams can change rapidly: these historic sites may have been subject to heavy sedimentation in the past but have since cleared up through recent years of reforestation and more conscientious land use practices in the sub-basin. Because rock size did not differ at the stream level it is reasonable to speculate that the patchy distribution of historic Eastern Hellbenders populations in the Upper Susquehanna sub-basin may have been shaped by the occurrence of abundant, large rocks. These so called “rock islands” may have become increasingly isolated and degraded by sedimentation. It remains unclear whether the elevated sediment load in the Upper Susquehanna sub-basin was primarily human-induced or if this is a natural characteristic of the system; evidence as to the pre-industrial character of the Upper Susquehanna sub-basin is the name Susquehanna itself, an Algonquian language group word that translates to “muddy current” (Kelton, 1888).

The Rusty Crayfish was by far the most widespread and abundant species at our sampling locations. This is consistent with long-term research by Kuhlman and Hazleton (2007) who found that the crayfish community in Upper Susquehanna sub-basin has significantly changed over the last 70 years. In addition to the Rusty Crayfish’s rise to dominance, Kuhlman and Hazleton (2007) failed to locate two crayfish species previously reported in the sub-basin (*O. limosus* and *O. immunis*). Although the Rusty Crayfish inhabits lower portions of the Susquehanna River watershed (Crocker, 1957) it was not present in the Upper Susquehanna

prior to 1991 (Kuhlman and Hazleton, 2007). Notably, Kuhlman and Hazleton (2007) also found that Rusty Crayfish can achieve much higher population densities than native crayfish with median density at sites with only the Rusty Crayfish estimated at 7.6 individuals/m² compared to sites with only the native Northern Clearwater Crayfish (*O. propinquus*) estimated at just 1.8 individuals/m².

The spread of the Rusty Crayfish poses several potential threats to Eastern Hellbenders. First, Eastern Hellbenders reportedly prefer to consume crayfish tail first (Netting, 1929), likely as a way to reduce a crayfish's ability to use its claws for defense. The claws-forward defensive posture adopted by Rusty Crayfish may reduce their palatability. Also, this species can rapidly out compete and replace native crayfish, which may be preferred Eastern Hellbender prey items, and has been found to reduce the abundance of macrophytes and macroinvertebrates where it has been introduced (Hobbs, 1989; Kuhlman and Hazleton, 2007). Last, the high densities attainable by Rusty Crayfish coupled with their aggressive nature may make the species a threat to Eastern Hellbender eggs and larvae. Behavioral experiments with captive Eastern Hellbenders and Rusty Crayfish are needed to elucidate the details of these species interactions.

A limitation of this study is the lack of habitat data from extant population sites. Examining habitat elements at historically occupied sites can be misleading, for example, crayfish community structure can change in as little as a year (Kuhlman and Hazleton, 2007). In addition, events such as fertilizer application to fields, near- or in-stream construction (Huckabee et al., 1975), and point source inputs of toxins from accidents (Peter Petokas, unpubl. data) can rapidly alter water chemistry for a short period after which conditions return to normal. Furthermore, the historic occurrence records (NYSDEC, 2006) used to locate

historic population sites did not contain information on population density or extent of occupied area, and site geographical locations were determined from landmarks, such as bridges. The accuracy of sampling site classification in the GIS model was limited by the coarse resolution of the land use data (30 m by 30 m) used to determine the presence of streamside forest cover. Despite using lack of forest cover as a criterion for selection, many “medium priority” sites did have a narrow band of trees between streams and uplands, while forested land at “high priority” sites typically extended farther upland.

Further research is needed to address a broader scope of potential causes of Eastern Hellbender decline and alternative search methods may prove to be more successful in locating extant populations. Rock lifting without the use of SCUBA is typically limited to water less than 1.5 m deep. Researchers have successfully used snorkeling (Nickerson and Mays, 1973a, b) and SCUBA (Peter Petokas, pers. comm.) to locate Eastern and Ozark Hellbenders in other regions, however the poor water clarity of the Upper Susquehanna sub-basin may confound this approach. Trapping has also been shown to be highly effective at capturing adult Eastern Hellbenders in the Allegheny drainages of New York State (Foster et al. 2008). It is also imperative to determine detection probabilities by conducting multiple site visits (5-10) at occupied locations in order to develop robust occupancy models. Findings from this work are consistent with previous Eastern Hellbender research on the habitat preferences of the species and indicate that habitat destruction is the most likely driver of Eastern Hellbender decline in the Upper Susquehanna sub-basin. Notably, the presence of an Eastern Hellbender under bank reinforcement “riprap” suggests that creating artificial refuge may be an effective conservation strategy for this habitat-limited species.

Table 1. Sources of geographical data used during the study of Eastern Hellbender distribution in the Upper Susquehanna sub-basin of New York State in 2008 and 2009.

Layer Type	Scale	Resolution	Projection	Date	Source
NLCD 2001	1:24,000	30 m	NAD 1983 Albers	2003	USGS Multi-Resolution Land Characteristics Consortium*
Hydrography	1:24,000	N/A	NAD 1983 Albers	2001	National Hydrography Dataset Cornell University Geospatial Information Repository**
Roads	1:24,000	N/A	NAD 1983 Albers	2001	

*<http://gisdata.usgs.gov/website/mrlc/viewer.htm>

**<http://cugir.mannlib.cornell.edu/>

Table 2. A list of the habitat variables compared across historically occupied and apparently unoccupied sampling areas visited during surveys for Eastern Hellbenders in the Upper Susquehanna sub-basin of New York State in 2008 and 2009.

Variable name	Description (units)
Shoreline cover	Percentage of canopy cover adjacent to sampling site (%)
Embeddedness	Percentage of stream substrate covered by soft sediments (%)
Crayfish relative frequency	Relative frequency of crayfish at a site determined by the percentage of occupied rocks (%)
Rusty crayfish relative frequency	Relative frequency of rusty crayfish at a site (%)
Native crayfish relative frequency	Relative frequency of native crayfish species at a site (%)
Minimum rock diameter	Minimum diameter of rocks examined (cm)
Mean summer Temperature	Mean temperature averaged from hourly records at sites from July to August 2008 (°C)
Temperature fluctuation	Range of temperature fluctuation at sites between July and August 2008 (°C)
pH	Mean pH at sites averaged from monthly samples taken in July, August, and September of 2008 and 2009 (pH)
Conductivity	Mean conductivity at sites averaged from monthly samples taken in July, August, and September of 2008 and 2009 (µS)

Table 3. Comparisons of forest cover and temperature profiles at the “high priority” sites (n = 19)—identified as being forested—and at “medium priority” sites (n = 10)—identified as lacking forest cover—visited during surveys for Eastern Hellbenders throughout the Upper Susquehanna sub-basin of New York State in 2008 and 2009. SD and CV are abbreviations for the standard deviation and coefficient of variation, respectively.

Variable Name	"High Priority" sites		"Medium Priority" sites		<i>Effect size (%)</i>	df	t	P
	Mean±1SD(n)	CV	Mean±1SD(n)	CV				
Mean cover (%)	0.38±0.19(19)	0.49	0.31±0.17(10)	0.54	22	27	0.9	0.38
Mean temperature (°C)	20.98±0.90(19)	0.04	21.12±0.37(10)	0.02	0.63	27	0.24	0.81
Temperature range (°C)	24.67±4.20(19)	0.17	20.17±9.57(10)	0.48	22.31	27	1.19	0.26

Table 4. Comparison of road density around bridge-centered sampling sites (“bridge”), randomly selected stream sites (“random”), and historically occupied Eastern Hellbender population sites (“historic”). Although bridge-centered sites were surrounded by more roads than randomly selected stream sites, road density was greatest near historic sites.

Site comparison	<i>effect size (%)</i>	df	t	<i>P</i>
Historic X Bridge	11.59	44	0.55	0.58
Historic X Random	186.56	44	4.33	< 0.001
Bridge X Random	156.52	44	4.28	< 0.001

Table 5. A summary of habitat covariates at historically occupied and apparently unoccupied Eastern Hellbender population sites (first tier) and stream systems (second tier) throughout the Upper Susquehanna sub-basin of New York State.

Variable Name	Historic		Non-Historic		<i>effect size (%)</i>	df	t	P
	Mean±SD(n)	CV	Mean±SD(n)	CV				
Shoreline cover	0.50±0.25(23)	0.51	0.36±0.19(36)	0.54	39.44	57.00	1.72	0.09
	0.43±0.21(44)	0.49	0.34±0.25(15)	0.73	26.98	57.00	1.35	0.18
Embeddedness	0.13±0.24(23)	1.80	0.31±0.29(36)	0.94	57.10	57.00	2.81	< 0.05
	0.22±0.26(44)	1.18	0.30±0.35(15)	1.17	25.25	57.00	0.95	0.35
Crayfish relative frequency	0.34±0.23(23)	0.68	0.26±0.21(36)	0.81	30.92	57.00	1.51	0.14
	0.31±0.22(44)	0.71	0.24±0.23(15)	0.94	28.63	57.00	0.91	0.37
Rusty crayfish relative frequency	0.48±0.37(23)	0.77	0.51±0.38(36)	0.75	5.31	57.00	0.54	0.59
	0.46±0.34(44)	0.74	0.58±0.45(15)	0.78	21.52	57.00	1.40	0.17
Native crayfish relative frequency	0.03±0.13(23)	3.94	0.05±0.17(36)	3.51	32.65	57.00	0.32	0.75
	0.03±0.10(44)	3.85	0.09±0.26(15)	2.80	71.74	57.00	1.53	0.13
Minimum rock diameter (cm)	42.43±14.38(23)	0.34	29.11±15.19(36)	0.52	45.76	57.00	3.35	< 0.001
	36.22±15.35(44)	0.42	28.68±17.64(15)	0.62	26.28	57.00	1.58	0.12
Mean temperature (°C)	21.68±1.04(23)	0.05	21.02±0.75(36)	0.04	3.15	57.00	1.84	0.08
	21.52±0.91(44)	0.04	20.87±0.94(15)	0.05	3.15	57.00	1.61	0.12
Temperature fluctuation (°C)	22.38±4.63(23)	0.21	23.65±5.57(36)	0.24	5.41	57.00	0.62	0.54
	22.11±5.14(44)	0.23	25.43±4.35(15)	0.17	13.05	57.00	1.51	0.15
pH	8.18±0.28(23)	0.04	8.22±0.24(36)	0.03	0.44	57.00	0.50	0.62
	8.19±0.27(44)	0.03	8.27±0.20(15)	0.02	0.96	57.00	0.92	0.36
Conductivity (µS)	261.99±58.34(23)	0.22	297.46±58.34(36)	0.20	11.92	57.00	2.20	0.03
	272.10±59.46(44)	0.22	325.67±44.43(15)	0.14	16.45	57.00	2.79	< 0.05

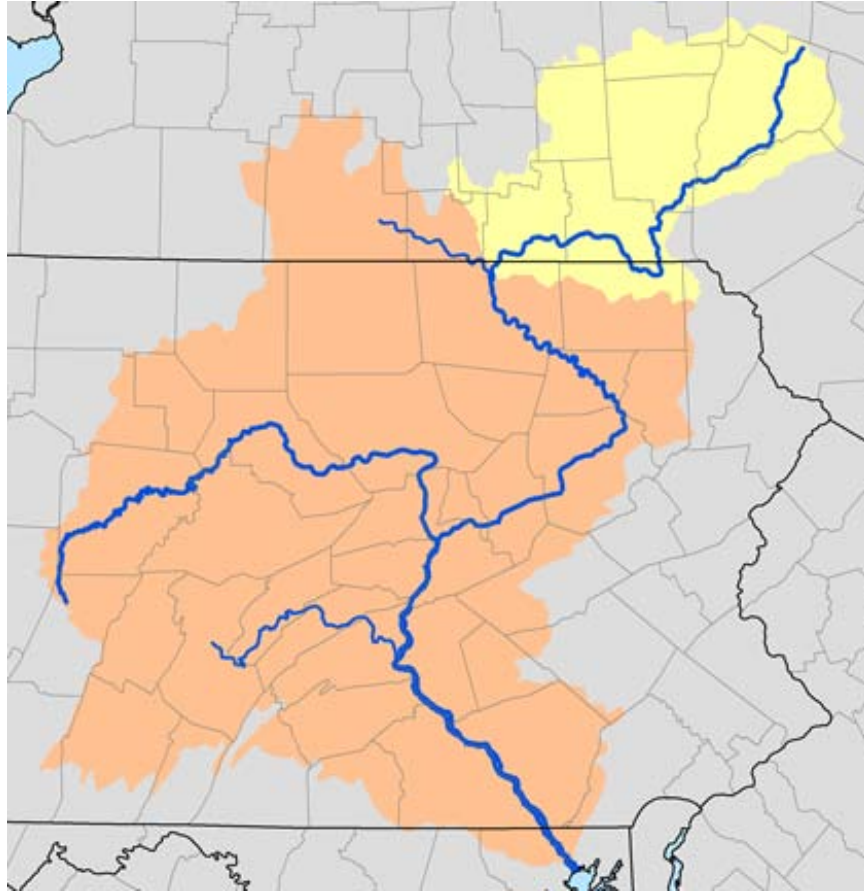


Figure 1. The Susquehanna River watershed colored orange and yellow. Surveys for Eastern Hellbenders in 2008 and 2009 were restricted to the Upper Susquehanna sub-basin (yellow), which encompasses the species' historic range in the Susquehanna River watershed of New York State.

CHAPTER 2: Geographical Determinants of Eastern Hellbender Distribution in the Northern Segment of its Range

Introduction

The Eastern Hellbender occurs from southern New York State to northern Alabama and west into Missouri, but despite this wide range local distribution is patchy and factors underlying population occurrence remain poorly known (Hillis and Bellis, 1971; Gates et al., 1985; Nickerson et al., 2003). Correlations have been made between population abundance and habitat elements (e.g. average rock size) within and among occupied sites (Hillis and Bellis, 1971; Nickerson et al., 2002; Nickerson et al., 2003), but there have been no studies to date examining the contribution of broad-scale environmental variables to population occurrence.

A more robust understanding of landscape influences on Eastern Hellbender distribution is needed because land use practices may contribute to population losses by accelerating sediment loading in streams and rivers (Ellis, 1936; Pimentel and Kounang, 1998; Wade and Heady, 2003). Sedimentation in particular is a serious threat to Eastern Hellbenders because it fills the narrow spaces under rocks that Eastern Hellbenders rely on for cover and has been blamed for the extirpation of many populations (Hillis and Bellis, 1971; Gates et al., 1985; Nickerson and Tohulka, 1986; Wheeler et al., 2003). Croplands are especially susceptible to soil erosion because traditional tillage completely eliminates cover, causing bare soil to intercept all of the rain and wind energy (Trimble and Crosson, 2000). Developed impervious surfaces can also accelerate sedimentation, in addition to affecting stream hydrology, by altering watershed responses to precipitation and snowmelt events (Swaney et al., 2006).

To date, predictive models have not been used to investigate the pattern of Eastern Hellbenders occurrence, yet this approach may be useful to examine the species at a regional

scale. Applications that predict a species' potential distribution by combining occurrence records with environmental variables have been used across a wide range of elusive species that occur in cryptic or difficult to sample habitats (Guisan and Thuiller, 2005; Pearson et al., 2007; Perkins et al., 2007). In addition, developing occupancy models for Eastern Hellbenders is difficult because it is impossible to thoroughly survey a stream without destroying habitat. Predictive modeling can help guide survey efforts, accelerating detection of unknown populations while also saving time and money (Raxworthy et al., 2003; Bourg et al., 2005). Matching occurrence records with environmental data also allows the importance of environmental features associated with Eastern Hellbender occurrence to be quantified, thereby enhancing our understanding of the habitat elements essential for population persistence. Predictive modeling has been effectively applied to support conservation planning for other cryptic species (Araujo and Williams, 2000; Ferrier et al., 2002), and can be used guide proposed Eastern Hellbender reintroduction programs. To this end, I examined Eastern Hellbender occurrence throughout the northern portion of their range in relation to 10 environmental variables. My objective was to create a predictive model of Eastern Hellbender occurrence and to quantify the relative contribution environmental variables to population occurrence.

Methods

Environmental coverages

I assembled 10 environmental coverages in ArcMap 9.2 (ESRI, Redlands, CA) relating to land use, topography, and climate covering Pennsylvania and the Susquehanna River watershed of New York State. Environmental coverages were available at fine- (1:24,000) and coarse-

(~1:2,000,000) scales (Table 1). Coarse-scale coverages were resampled to 0.005 dd (~500 m by ~400 m), considered an appropriate Minimum Mapping Unit (MMU) size for 1:2,000,000 or smaller scale environmental data (Veg MOU workgroup, 2002). Coarse-scale layers were then clipped to a 1 km buffer of the National Hydrography Dataset (Simley and Carswell, 2009). Fine-scale layers (resolution 30 m by 30 m) were clipped to a 100 m buffer of the National Hydrography Dataset (Simley and Carswell, 2009). First order and ephemeral streams were excluded from the analyses.

Data on surficial geology (Fullerton et al., 2004), and landslide susceptibility (Godt, 2001) were obtained from the USGS data archive (<http://www.nationalatlas.gov>). Population occurrence appears to be dependent on the presence of the large, flat rocks that Eastern Hellbenders use for cover (Gates et al., 1985; Nickerson and Tohulka, 1986; Wheeler et al., 2003), therefore examining regional geology may elucidate the geologic conditions that generate appropriate cover rocks. Landslide susceptibility in particular may serve to identify areas conducive to forming large rock deposits because this variable was based largely on the frequency historic landslide events. Moreover, populations in the Allegheny River watershed of New York State tend to occur at the base of steep, rocky slopes (Kenneth Roblee, unpubl. data), which may reflect a specific landslide susceptibility category. Data on land cover and elevation were extracted from the Multi-Resolution Land Characteristics Consortium's National Land Cover Database 2001 (2001 NLCD) (Homer et al., 2004; <http://www.mrlc.gov>). Land cover was resampled into a forest layer and a developed layer detailing the percent cover type of each land use category. Elevation and the extent of upstream forest cover have been shown to be related to Eastern Hellbender abundance (Humphries, unpubl. data).

I extracted temperature data from the WorldClim database (Hijmans et al., 2005; <http://www.worldclim.org>) that were generated through interpolation of weather station data on a 30" grid and represent average conditions from 1950 to 2000. In addition to the annual average, I organized the temperature data into categories assumed to be ecologically relevant to Eastern Hellbenders: winter (November – February), spring (March – June), and summer (July – October), which encompasses the breeding period (Gibbs et al., 2007). Average annual precipitation data from the period of 1961-1990 (Daly and Taylor, 2000) were downloaded from the USGS data archive (<http://www.nationalatlas.gov>). Air temperature, which I used as a characterization of water temperature, was included because Eastern Hellbenders tend to be found in cool water streams (Hutchison et al., 1973).

Modeling the geographical distribution of the Eastern Hellbender

I used a correlative approach to model Eastern Hellbender distribution by linking population occurrence, based on locality data from Pennsylvania (n = 59) (Pennsylvania Natural Heritage Program; Peter Petokas, unpubl. data), to environmental data coverages (Table 1). More specifically, I used the MaxEnt (Phillips et al., 2006; <http://www.cs.princeton.edu/~schapire/maxent>) maximum entropy algorithm (Version 3.3.1) to characterize species distributions from presence data and environmental layers of identical resolution and extent, which is an ideal approach for elusive species such as the Eastern Hellbender that lack reliable absence data. MaxEnt does not directly predict probability of occurrence, rather a suitable geographic range based on the modeled ecological niche of the species (Phillips et al., 2006). The MaxEnt approach was chosen because it has been shown to

consistently out perform other modeling approaches, especially at predicting excluded localities (Elith et al., 2006; Phillips et al., 2006; Pearson et al., 2007).

Two scale-distinct models were created to avoid conflating issues of mapping differently scaled coverages with model performance and to determine whether coarse- versus fine-scale environmental variables were better predictors of Eastern Hellbender habitat suitability. One model used fine-scale data: elevation, percent forested cover and percent developed cover. The second model used coarse-scale data: surficial geology, landslide susceptibility, mean annual precipitation, and annual and seasonal temperature averages. I used the recommended MaxEnt default settings for the convergence threshold (10^{-5}), maximum number of iterations (500), and output (logistic). Twenty-five percent of training sites were set aside to act as validation, or test, sites. The importance of environmental variables was determined using MaxEnt's jack-knife procedure, in which each variable was analyzed singly then removed from the dataset to determine model building contribution and how much "unique" information each contained. Model performance was evaluated using the Receiver Operating Characteristic (ROC) method, an approach that has recently become prevalent in ecological applications (Giovannelli et al., 2008; Wang and Li, 2009), in which an Area Under Curve (AUC) value of 0.7–0.8 represents acceptable models; values of 0.8–0.9 represent excellent models; and values greater than 0.9 represent outstanding models (Hosmer and Lemeshow, 2000). MaxEnt determines the test AUC value by comparing the overall fraction of background pixels predicted as "present" to successfully locate pixels containing test sites. A high AUC value is achieved when fewer background pixels are needed to predict the location of test sites.

Results

Model performance

The Eastern Hellbender predictive model generated using coarse-scale environmental data achieved an AUC value = 0.889, which demonstrated that performance was satisfactory; the test AUC was also high (AUC = 0.837, SD = 0.050) (Fig. 1). Test data were predicted better than random with the same fractional predicted area (omission rates for all but one threshold achieved significant ($P < .05$) 1-sided P-values). The fine-scale model achieved an AUC value = 0.778; test AUC = 0.805 (SD = 0.046) (Fig. 2). Test data could not be predicted better than random at the more conservative thresholds (i.e., minimum training presence).

Environmental drivers of Eastern Hellbender distribution

Landslide susceptibility and surficial geology contributed the most information to the coarse-scale model (49.4% and 30.6% respectively) (Table 2). Surficial geology achieved the highest gain when used in isolation while landslide susceptibility decreased gain the most when omitted. Three of the 30 material types in the surficial geology coverage were identified as being particularly important contributors to population occurrence: loamy till, clayey to loamy till, and mixed origin sand and gravel deposits. These material classes are uncommon on the landscape, each comprising only ~1% of the total coverage. Most presences occurred within regions “moderately susceptible” to landslides where 1.5 - 15% of the area has been involved in sliding—a comparatively high historic incidence. Annual precipitation data contributed 17.2% to the coarse-scale model while the other climatic variables were generally poor predictors of hellbender occurrence ($\leq 2.2\%$).

In the fine-scale model, percent forested cover contributed the most information (40.6%) (Table 3). Highest suitability appeared to increase at lower altitudes and within areas with the most forest coverage. Similarly, areas with the lowest percentage of developed land were considered most suitable.

Discussion

My research indicates that surficial geology is an important driver of Eastern Hellbender occurrence in the northern portion of their range. The two coarse-scale variables with the most explanatory power—surficial geology and landslide susceptibility—are features that characterize surface rock formations. These geological features have a direct linkage to Eastern Hellbender habitat requirements, that is, the presence of large, flat rocks (Noeske and Nickerson, 1979; Soule and Lindberg, 1994; Quinn, unpubl. data). Surficial geology data provides information on the cover material potentially available to Eastern Hellbenders, while landslide susceptibility may serve to identify areas where these materials were deposited in rivers and made accessible. Other researchers have noted that so-called “rock islands” favored by Eastern Hellbenders are typically found at the base of steep hillsides (Kenneth Roblee, unpubl. data; Peter Petokas, unpubl. data).

Also significant is the rarity of the three most suitable surficial geology classes (each ~1% of total coverage), suggesting that Eastern Hellbender occurrence may be dependent not only on the availability of cover rocks, but on the geologic character of the area which may contribute more to habitat quality than shelter. For example, these surficial material classes are relatively coarse textured, perhaps indicating that silt and other fine particles known to cause

the greatest impact on Eastern Hellbender habitat are rare in the area, thus potential upland sediment inputs may not be as harmful.

Further resolution of how land use practices contribute to Eastern Hellbender declines, and therefore might be the target of regulation and management, is needed. Notably, relative abundance of Eastern Hellbenders across 21 sites in Georgia decreased as the proportion of agriculture within 300 m of stream increased, and populations downstream from more than 25% agricultural land were extirpated (Jeffrey Humphries, unpubl. data). While I did not find land use variables to be strongly related to occurrence, certain practices may influence population persistence. Percent forested land has been used as an index of anthropogenic disturbance (Houlahan and Findlay, 2003) and can serve as an indicator of habitat quality. For example, percent forested land upstream from population sites in Georgia was the best indicator of Eastern Hellbender abundance (Humphries, unpubl. data). Future research on the regional distribution of Eastern Hellbenders should incorporate abundance data that can act as an index of the influence of land use near populations.

Forested riparian buffers may be critical to Eastern Hellbender conservation. Riparian buffers trap sediments and pesticides from upland sources (Smith and Minton, 1957; Williams et al., 1981; Trimble, 1999), thus can serve as a management strategy to maintain high quality Eastern Hellbender habitat. However, consideration of riparian buffers as an Eastern Hellbender conservation strategy should be tempered by the fact that the mere presence of a buffer zone does not guarantee sediment trapping: multiple elements must be considered when determining the effectiveness of a buffer including width, vegetation type, and slope. In a review of more than 80 articles on the factors influencing buffer efficacy, Liu et al. (2008) found that buffer slope and width were most important in determining sediment-trapping

effectiveness. Also, while most states require a riparian buffer zone between streams and uplands enforcement is not universal, and the function of a buffer is nullified if sediments are being added upstream.

Predictive models performed well and demonstrated that a habitat modeling approach can be useful for Eastern Hellbender habitat management by identifying regions of suitable habitat. However, model output should be interpreted cautiously because some environmental coverages appeared spatially autocorrelated, e.g., seasonal temperature averages. Because correlated variables provide similar information their combined effect at the cell level can appear very small and therefore may not accurately represent each variable's influence on habitat suitability (Phillips et al., 2006). Furthermore, presence records reflected the current clustered nature of Eastern Hellbender distribution and tended to occur in small (~500 m) stream segments. If hellbenders have declined disproportionately in lower order streams then current distributions may not provide an ideal basis for predicting range-wide distribution patterns.

The coarse-scale model performed better than the fine-scale model, and results indicated that variables related to topography—surficial geology and landslide susceptibility—were identified as the best predictors of suitability. Comparison of model predictive power (AUC value) should be tempered by the fact that both models accurately assigned highly suitable ratings to pixels containing test sites and historically occupied New York State sites. The fine-scale model achieved a lower AUC value because its prediction of habitat suitability was less concentrated than the coarse scale model, meaning that a greater number of background pixels had to be predicted as suitable to successfully identify all of the pixels containing test sites.

Eastern Hellbenders may be particularly sensitive to extinction due to their sensitivity to habitat alteration and naturally fragmented distribution resulting from an apparent reliance on specific and uncommon geologic conditions. Future research into the drivers of Eastern Hellbender distribution would benefit from the inclusion of range-wide presence data coupled with population abundance estimates that can act as indices of habitat quality. My work has shown that predictive modeling can serve as a powerful tool with which to identify high priority habitat areas and thereby direct conservation strategies to more efficiently address the rapid range-wide decline of Eastern Hellbenders.

Table 1. Environmental coverages used to develop the MaxEnt predictive models of Eastern Hellbender habitat suitability in their northern range segment.

Layer Type	Scale	Resolution	Date	Source
Hydrography	1:24,000	N/A	2001	National Hydrography Dataset
Topography				
Surficial materials/deposits	1:2,500,000	N/A	2004	USGS National Atlas
Landslide susceptibility	1:4,000,000	N/A	2001	USGS National Atlas
Elevation	1:24,000	30 m	2007	NED
Climate				
Mean annual temperature	1:2,000,000	30"	2005	WorldClim
Mean summer temperature	1:2,000,000	30"	2005	WorldClim
Mean winter temperature	1:2,000,000	30"	2005	WorldClim
Mean spring temperature	1:2,000,000	30"	2005	WorldClim
Mean annual precipitation	1:2,000,000	N/A	2000	USGS National Atlas
Land Use				
Percent forest cover	1:24,000	30 m	2003	2001 NLCD
Percent developed cover	1:24,000	30 m	2003	2001 NLCD

Table 2. Contributions of coarse-scale ($\leq 1:2,000,000$) environmental variables to the occurrence of Eastern Hellbender populations in their northern range segment as derived from jack-knifing in the MaxEnt algorithm.

Variable	Contribution (%)
Landslide susceptibility	49.4
Surficial geology	30.6
Mean Annual Precipitation	17.2
Mean winter temperature	2.2
Mean annual temperature	0.5
Mean spring temperature	0.1
Mean summer temperature	0

Table 3. Contributions of fine-scale (1:24,000) environmental variables to the occurrence of Eastern Hellbender populations in their northern range segment derived from jack-knifing in the MaxEnt algorithm.

Variable	Contribution (%)
Percent forest cover	40.6
Percent developed cover	35.7
Elevation	23.7

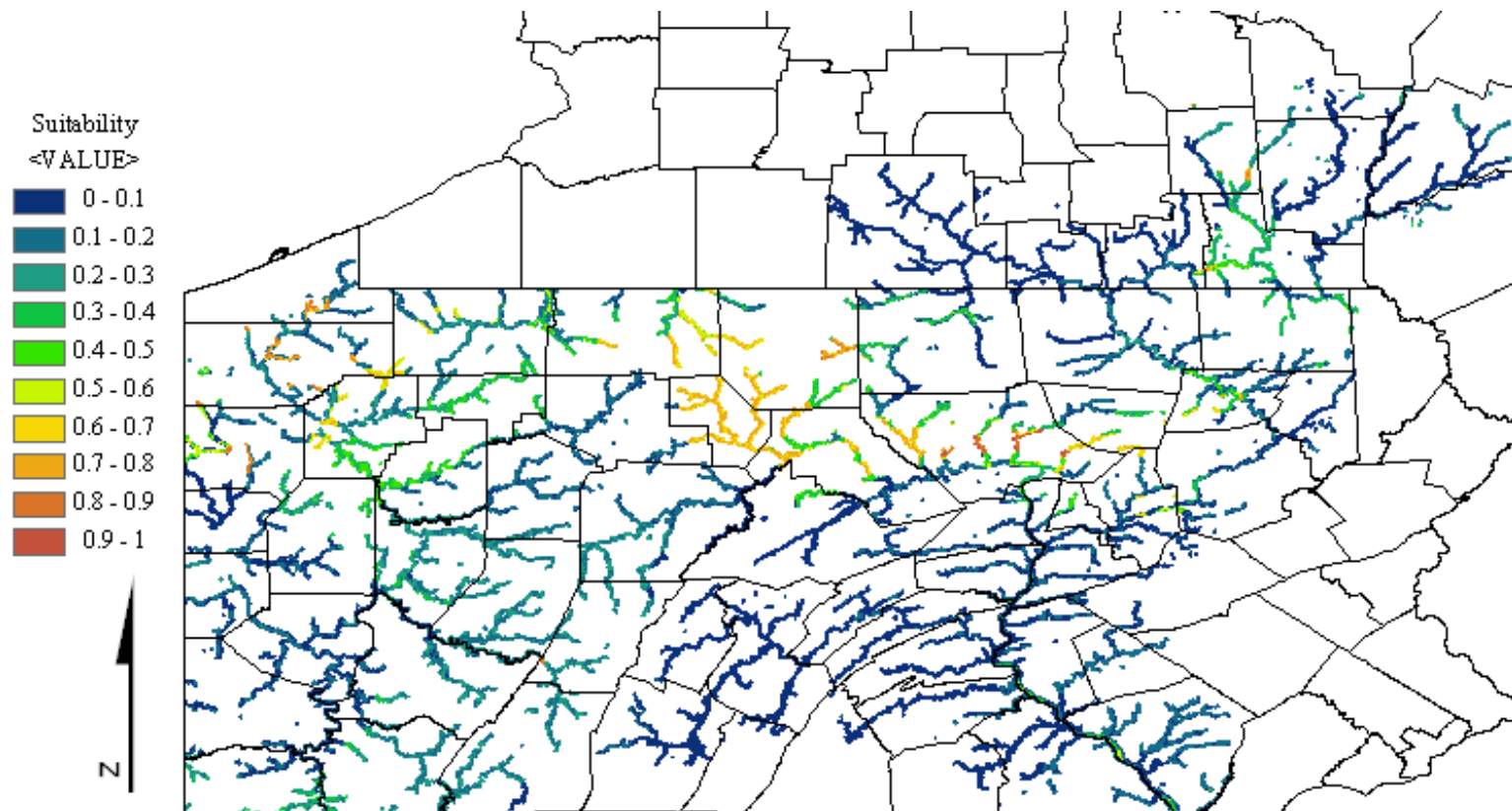


Figure 1. Predicted suitability of Eastern Hellbender habitat in Pennsylvania and the Susquehanna River watershed of New York State based on locality data from Pennsylvania and coarse-scale ($\leq 1:2,000,000$) environmental coverages: surficial geology, landslide susceptibility, mean annual precipitation, and annual and seasonal temperature averages. One indicates highest suitability, 0 is least suitable. The locations of sites used to develop the suitability map are not shown due to the species' sensitivity to illegal collection.

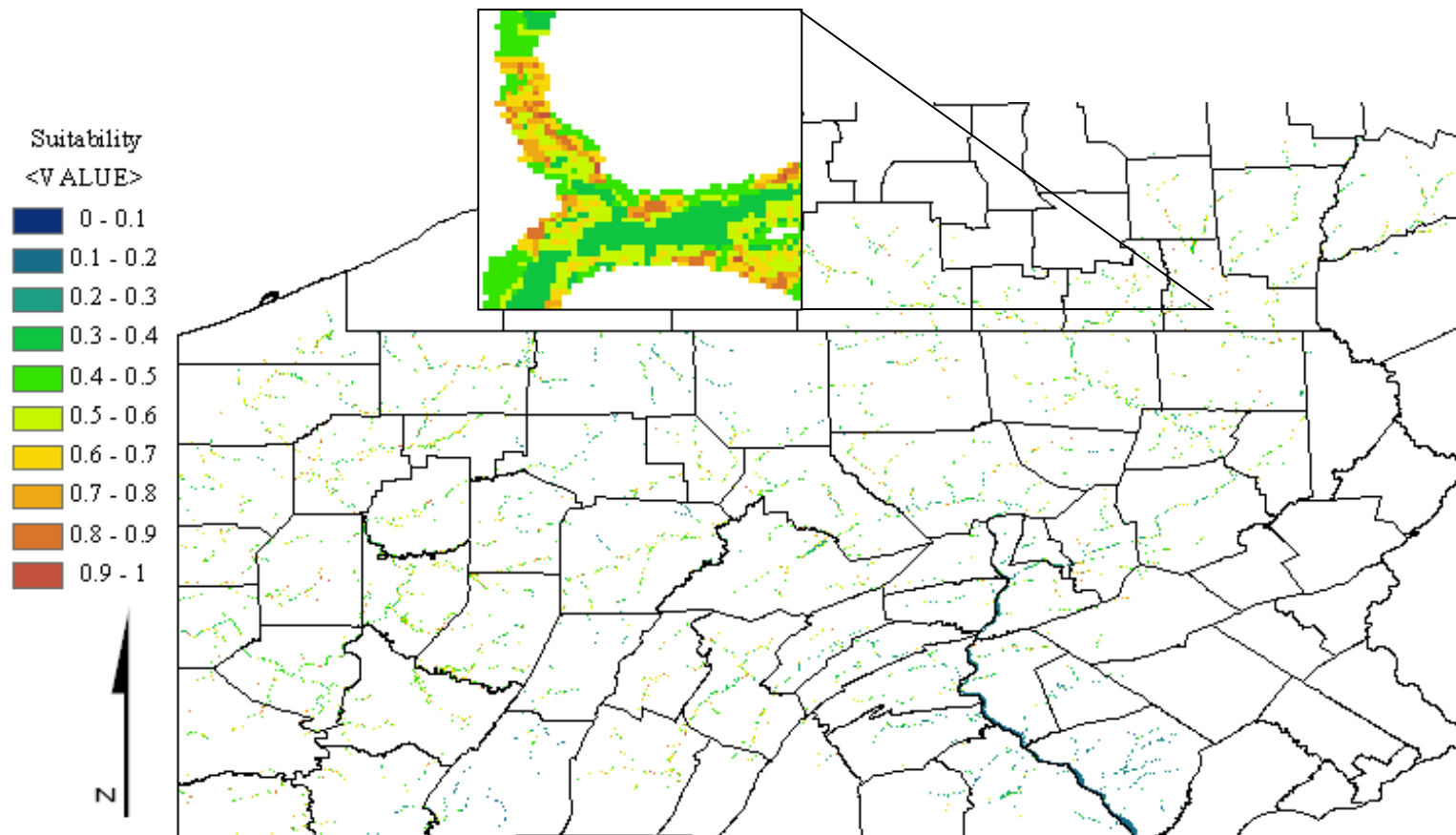


Figure 2. Predicted suitability of Eastern Hellbender habitat in Pennsylvania and the Susquehanna River watershed of New York State based on locality data from Pennsylvania and fine-scale (1:24,000) environmental coverages: elevation, slope, percent forested cover, and percent developed cover. One indicates highest suitability, 0 is least suitable. The inset is zoomed-in on the intersection of the Chenango River with the Susquehanna River at Binghamton, NY to show detail.

CONCLUSIONS

My research has shown that the distribution of Eastern Hellbenders in their northern extent is strongly related to the presence of specific and uncommon geologic conditions. By comparing habitat elements across historically occupied and apparently unoccupied population sites I conclude that the historic occurrence of Eastern Hellbender in the Upper Susquehanna sub-basin of New York State was driven by the presence of large rock deposits. Furthermore, contrasting rock size at historic population sites and non-historic sites suggests that quality habitat is rare in the Upper Susquehanna sub-basin. Although large rock deposits may have been naturally uncommon in the sub-basin, it is possible that adequate cover rocks were buried by decades of sedimentation related to agricultural development. Eastern Hellbender declines may have also been accelerated by the introduction of the Rusty Crayfish to the Upper Susquehanna sub-basin. The aggressive behavior of the Rusty Crayfish, in addition to its tendency to reach high population densities, could make this crayfish unpalatable to adult Eastern Hellbenders and a significant predator on Eastern Hellbender eggs and larvae. Behavioral experiments are needed to determine the details of these species interactions.

Examination of the geographical determinants of Eastern Hellbender distribution also showed correlations between population occurrence and specific geologic features. Moreover, geologic features are more strongly related to population occurrence than the other environmental factors examined, further evidence that Eastern Hellbender distribution is determined by the occurrence of specific geologic conditions. Although land use variables were not strongly related to Eastern Hellbender occurrence certain land use practices may affect population abundance by contributing to the stream sedimentation known to degrade habitat.

My work suggests that Eastern Hellbenders are particularly vulnerable to extinction because of the rarity of their preferred habitat and sensitivity to sedimentation conferred upon them by a highly fragmented distribution. Conservation planning would benefit from the use of predictive models as a means to examine regional habitat suitability thereby focusing survey efforts for unknown populations and guiding reintroduction programs. The creation of artificial habitat may be an effective conservation strategy because Eastern Hellbenders appear to be habitat limited and will apparently colonize artificial cover such as the riprap commonly used in bridge construction.

Eastern Hellbender may soon be completely extirpated from the Upper Susquehanna sub-basin. This alarming trend appears to be driven by habitat destruction in the form of sedimentation, which is possibly linked to certain land use practices. Managers in regions where populations remain robust should act to mitigate sedimentation in order to maintain the quality stream habitat essential to the persistence of Eastern Hellbender populations.

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