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Historical Evidence on the Origins of Eastern Hellbenders (*Cryptobranchus alleganiensis*) in the Susquehanna River Watershed, Eastern USA

Robin L. Foster[1,2,5], Chris P.S. Larsen[3], and Amy M. McMillan[4]

[1]*Graduate Program in Evolution, Ecology and Behavior, State University of New York, University at Buffalo, 373 Cooke Hall, Buffalo, New York 14260, USA*

[2]*Department of Animal Behavior, Ecology, and Conservation, Canisius College, 2001 Main Street, Buffalo, New York 14208, USA*

[3]*Department of Geography, State University of New York, University at Buffalo, 124 Wilkeson Quad, Buffalo, New York 14261, USA*

[4]*Department of Biology, State University of New York, Buffalo State University, 1300 Elmwood Ave., Buffalo, New York 14222, USA*

[5]*Corresponding author, e-mail: foster32@canisius.edu*

Abstract.—**The Eastern Hellbender (*Cryptobranchus alleganiensis*) is a fully aquatic salamander endemic to eastern North America. Although hellbenders are found primarily in watersheds connected to the Mississippi River, a disjunct population is present in the Susquehanna River Basin. The origin of this population has long been the subject of speculation, with stream capture as the commonly hypothesized mechanism of introduction. We employed a novel approach using historical sources to assess the origin of Susquehanna hellbenders, specifically archaeological, paleontological, and archival evidence. Hellbender remains were absent from all prehistoric assemblages in the Susquehanna River watershed, despite being present in more than 75% of assemblages from sites within other portions of the known hellbender range. Archival records failed to reveal any hellbender occurrences in the Susquehanna River watershed prior to the 1830s, and the spatial and temporal pattern of sightings indicates a slow spread throughout the watershed initiating at two separate points of entry: an initial colonization along the Allegheny divide that may support the hypothesis of a natural range expansion, and a secondary colonization in the lower reaches of the Susquehanna River that suggests anthropogenic transportation of the species. Disjunct populations may have important value for conservation due to the unique ecological and evolutionary conditions they experience. Further study on the role and adaptations of hellbenders to conditions in the Susquehanna ecosystem may provide important insights on their conservation, regardless of their origin.**

Key Words.—Caudata; conservation; disjunct population; freshwater; historical ecology; range expansion; salamander

Introduction

The origins of disjunct populations are of interest from both biogeographical and conservation perspectives. Two mechanisms can generally be invoked to explain disjunct distributions: vicariance, in which the continuous range of ancestral forms is divided by environmental or geological events, and natural or anthropogenic dispersal, in which the distribution is caused by movement across a geographic barrier (Ronquist 1997). Disjunct populations may experience different ecological conditions and evolutionary trajectories as compared with those in the core range, resulting in the need for differing management approaches. Additionally, distinguishing between natural range expansions and human-mediated movements may be an important consideration for conservation decision-making.

The Eastern Hellbender (*Cryptobranchus alleganiensis*; hereafter hellbender) is a fully aquatic salamander found in portions of the Mississippi and Susquehanna River watersheds in the eastern USA (Petranka 1998; Fig. 1). Although their numbers have declined substantially across their range over the past several decades (Wheeler et al. 2003; Foster et al. 2009; Burgmeier et al. 2011b), hellbenders were known to be abundant historically in some Mississippi tributary systems, including the Ohio River watershed and one of its main subbasins, the Allegheny River watershed (Bishop 1941; Swanson 1948; Mayasich et al. 2003). Hellbender distribution within the disjunct Susquehanna River Basin is much more limited, with occurrences reported from a relatively small number of Susquehanna tributaries and high abundances observed in few areas (New York Natural Heritage Program data set; Pennsylvania Natural Heritage Program data set).

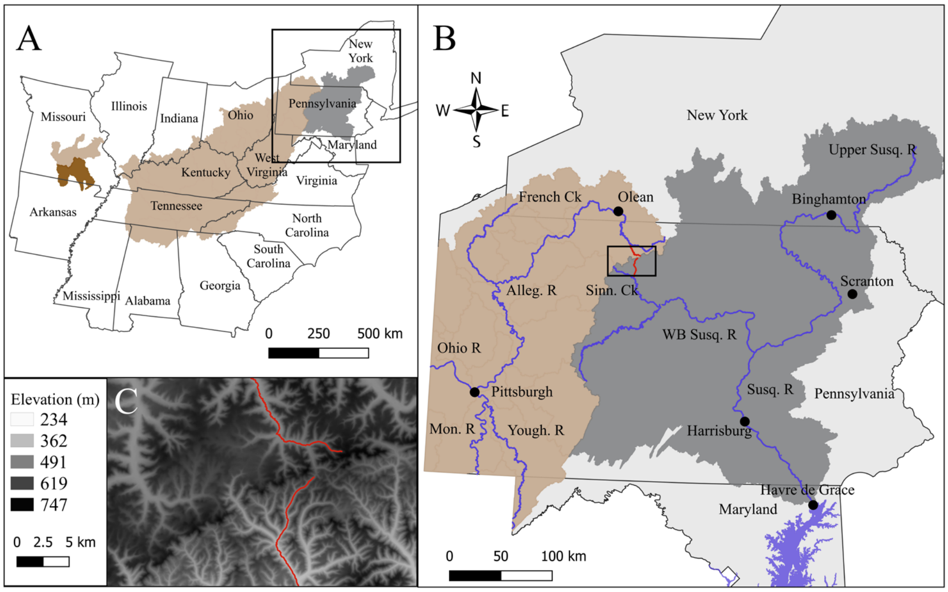

Figure 1. Maps indicating study area and key geographic features of (A) Modern range of Eastern Hellbenders (*Cryptobranchus alleganiensis*; https://doi.org/10.5066/F7BR8R7K) in the USA. Only states within the modern range of *C. alleganiensis* are shown. Core range is displayed in light brown and disjunct Susquehanna River watershed is displayed in gray. Dark brown indicates range of the Ozark hellbender subspecies (*C. a. bishopi*). Light gray shading indicates areas within the Mississippi watershed, but not within the known range of *C. alleganiensis*. Black box indicates the location of the map displayed in panel B. (B) Focal area of historical study surrounding the divide between the Ohio and Susquehanna watersheds. Streams shown in red indicate the closest approach between these two watersheds. Black box indicates the location of the map displayed in panel C. Abbreviations for major river names are Alleg = Allegheny, Mon = Monongahela, NB = North Branch, Sinn = Sinnemahoning, Susq = Susquehanna, WB = West Branch, and Yough = Youghiogheny. (C) Elevation map of divide between watersheds at their closest approach. This area represents the most likely location for a natural colonization through drainage rearrangement.

Hellbenders have been the subject of intensive conservation efforts in parts of the Susquehanna watershed due to reports of substantial declines (Breisch 1990; Mayasich et al. 2003; Quinn et al. 2013). The watershed is of particular interest because it includes both the northernmost and easternmost points of the range of the species, and it experiences a high level of threat from development and water pollution. For example, a 2016 pipeline rupture spilled 207,000 L of gasoline into the West Branch of the Susquehanna in Pennsylvania. Although the event does not appear to have extirpated hellbenders from the area, the long-term effects of such catastrophes remain uncertain (Perelman et al. 2021).

The origin of populations of hellbenders in the Susquehanna River watershed has long been the subject of speculation. Surface (1913) described the native range of the hellbender as encompassing the Ohio Valley and areas south. He hypothesized that to enter streams east of the Allegheny Mountains, hellbenders may have crossed between watersheds during a temporary hydrologic connection at an elevated swamp. Both Netting (1932) and Arthur Hulse (unpubl. report) suggested that hellbenders may have traveled to the Susquehanna River through a relatively recent stream capture event, in which a stream is diverted in a manner that causes it to flow into an adjacent watershed. Both scenarios represent forms of drainage rearrangement: a natural reorganization of river systems that can occur through channel migration, tectonic activity, or catastrophic flows (Bishop 1995), and would suggest a natural range expansion for hellbenders entering the Susquehanna. Little evidence, however, has been presented to determine whether hellbenders are, in fact, a recent arrival to the Susquehanna and whether they arrived through natural or anthropogenic mechanisms.

Population genetic studies and phylogeographic methods are commonly employed to investigate population origins (Avise 2009; Habel et al. 2015). Because of their rarity, few hellbenders from the Susquehanna River watershed have been included in genetic analyses. Population genetic studies that have included Susquehanna samples have consistently shown a close relationship between hellbenders from the Susquehanna River watershed and those from the Ohio River watershed (mitochondrial DNA: Sabatino and Routman 2009; microsatellite DNA: Tonione et al. 2011; Unger et al. 2013; genome-wide DNA: Hime 2017), although Susquehanna hellbenders are genetically distinct (mitochondrial DNA: Rayman 2010; microsatellite DNA: Unger et al. 2013; 2016). Analysis of a subset of range-wide genomic data by Hime (2017) showed that hellbenders from the Susquehanna are very closely related to those from the Allegheny/Ohio river watershed. In addition, Susquehanna hellbenders had a small number of private alleles and relatively low polymorphism as compared with those from other areas of the range of hellbenders (Paul Hime, pers. comm.). These data may suggest a recent origin of hellbenders in the Susquehanna River watershed, and/or multiple colonization or introduction events. The small number of samples available from the Susquehanna watershed, however, limits the ability of these studies to determine where hellbenders entered the Susquehanna and when or how that may have occurred.

In the absence of sufficient genetic data, there are few methods available to assess the origins of disjunct wildlife populations. Here we employ a novel, alternative approach to investigating the origins of Susquehanna hellbenders based on historical information. Using archival, archaeological, and paleontological sources, we aim to identify the earliest records of hellbenders in the Susquehanna River watershed, track the pattern of sightings throughout the watershed over time, and seek evidence to support or refute the hypothesis of a recent introduction by natural or human-mediated dispersal. Improving our understanding of the historical relationship between hellbender populations in the Mississippi and Susquehanna River watersheds will fill a key knowledge gap about this species and have important implications for conservation planning.

Materials and Methods

***Study area*.—**For this study, we defined the core range of hellbenders as all river systems with records of hellbender presence that are hydrologically connected to the Mississippi River watershed, and the disjunct range as the Susquehanna River and its tributaries. To assess the extent of past distribution of hellbenders, we examined three types of historical data. The first two datasets were explored across all U.S. states containing any part of the core or disjunct range (Fig. 1). These data included records of prehistoric remains of *Cryptobranchus* from archaeological and paleontological sources, and historical descriptions of the known range of hellbenders from natural history sources. The third dataset, containing location-specific occurrence records of hellbender sightings, focused on the region surrounding the topographic divide between the Ohio and Susquehanna River basins, a region encompassing these rivers and their tributaries in New York State, Pennsylvania, and Maryland (Fig. 1). This area was selected because it includes all potential locations where drainage rearrangement or human-mediated dispersal may have taken place. The disjunct and core ranges make their closest approach at the headwaters of the Allegheny Portage and Sinnemahoning Portage creeks, where < 5 km separates these streams (Fig. 1B, C; shown in red). Although the watersheds are divided by a high-elevation ridge, this barrier is interrupted by areas of mid-elevation wetland (Fig. 1), which may have formed the basis of the hellbender dispersal hypothesis first proposed by Surface (1913).

***Focal taxonomic lineage*.—**There are currently two recognized subspecies of the hellbender, the eastern subspecies (*C. a. alleganiensis*), which has historically occupied the eastern U.S. from New York to Missouri and south to Georgia, and the Ozark subspecies *(C. a. bishopi)*, which is restricted to the Ozark highlands of southern Missouri and northeast Arkansas (Fig. 1). Recent genomic analysis, however, suggests that *Cryptobranchus* contains as many as five evolutionarily distinct lineages: (1) the White and Black River drainages in the Ozarks; (2) Kanawha and New River drainages; (3) Tennessee River drainages; (4) Ohio, Allegheny, and Susquehanna River drainages; and (5) Missouri, Mississippi, and Green River drainages (Hime 2017). The hellbender populations of interest for our study fall within the current *C. a. alleganiensis* subspecies and the proposed Ohio/Allegheny/Susquehanna clade.

***Archaeological and paleontological evidence*.—**To assess the prehistoric distribution of hellbenders, we conducted an internet search to locate archaeological and paleontological sources containing complete faunal analyses, including herptiles identified to genus. Because the bones of small animals often do not survive for long periods of time, herptiles are sometimes excluded from archaeofaunal descriptions or grouped under a generic category such as fish or turtle (Olsen 1968). To locate records that included the appropriate level of identification detail, we used search terms including the common and scientific names not only of the hellbender, but also of several common amphibian species, including the American Bullfrog (*Rana catesbieana*/*Lithobates catesbieanus*) and American Toad (*Bufo americanus*/*Anaxyrus americanus*), and several common amphibian genera (*Rana*/*Lithobates*, *Plethodon*, *Bufo*/*Anaxyrus*, and *Ambystoma*).

For each list of faunal remains found to include amphibians identified to genus or species, we recorded the following: (1) *Cryptobranchus* presence or absence; (2) approximate age of the site; (3) approximate location of the site; (4) watershed; and (5) whether the location is within the current range of *C. alleganiensis*. We classified sites as archaeological if the herpetofaunal assemblage was associated with an archaeological site, and paleontological if it was not. We estimated location based on site description when precise coordinates were not provided. We mapped locations against the current range of *C. alleganiensis* using QGIS 3.16 (www.http://qgis.osgeo.org) for comparison. For a complete list of 81 archaeological and paleontological sites and sources, see Supplemental Information Part 1.

Historical range descriptions.—We collected natural history accounts of hellbenders through searches of 16 online archival databases, bibliographic search engines, and newspaper databases (Supplemental Information Part 2). Each contained a variety of natural history texts, encyclopedias, and periodicals. To locate entries related to hellbenders, we searched for 11 current and historically used common and scientific names of the species. When a search returned more than 1,000 hits, we narrowed the search using keywords related to range or distribution. We retained any source containing a description of the range of the species (e.g., "Hellbenders are found only west of the Allegheny Mountains") or a range map. Because some common names may refer to more than one species, we used additional information in the source (such as physical description of the animal) to eliminate any accounts that were not clearly referring to hellbenders. For each source, we recorded the date of the account and whether the source considered hellbenders to be present, rare, or absent from the core range and the Susquehanna watershed at the time it was written. We determined rarity in a watershed, which may indicate a population expanding into new areas or one that is in decline, based on the description. We interpreted phrases such as rare, occasionally found, or almost unknown from as indicators that hellbenders were present but not common in a particular area. We grouped sources in 25-y time intervals, ending in 1975. By the mid-1970s, scientific studies had provided clear information about hellbender distribution, and their presence in both the core range and Susquehanna River watershed was well known (Nickerson and Mays 1973).

Location-specific occurrence records.—We collected records of location-specific hellbender sightings and indicators of relative abundance (e.g., "34 hellbenders were collected from the Ohio River near Pittsburgh in 1833") from the earliest available records through 1999 in New York, Pennsylvania, and Maryland (Fig. 1). We found archival historical sources, such as newspapers, natural history and local history texts, periodicals, books, and scientific articles by searching online archival databases, bibliographic and genealogical search engines, and newspaper archives. Each was searched using all possible combinations of hellbender names and location terms, which included state and watershed names. We also obtained records from museum collections via vertnet.org and through the Natural Heritage Program of appropriate states (Supplemental Information Part 2). Sources for location-specific occurrences are not provided to protect sensitive locations.

For each location-specific account of hellbender occurrence, we recorded the date, location, and number of animals reported. If the actual number of animals was not included in the account, we made an estimate using indicators of relative abundance in the text of the report. We counted the description of a couple as two animals, a few as three, some or several as five, and many, numerous, or other words indicating high abundance as 10 animals. If no indication of the number of animals was provided, we counted the occurrence as a single animal. We grouped historical occurrences into 50-y time intervals, from 1800 to 1999, with the small number of records dated prior to 1800 grouped into the earliest time interval (pre-1800 to 1849). We obtained county-level human population records for each time interval from the Historic County Boundaries and Total Population, United States dataset (www. https://geo.nyu.edu/). Because population data were not available for all years, and county boundaries changed from year to year, population records from the first available year of each time interval were used. We mapped occurrence records of hellbenders over human population density using QGIS 3.16.

Results

Archaeological and paleontological evidence.—We identified 46 archaeological sites with complete faunal analyses within the current known range of *C. alleganiensis*: 37 in the core range and nine in the Susquehanna River watershed. Six paleontological deposits were found with amphibian assemblages identified: four in the core range and two in the Susquehanna watershed (Fig. 2). Most sites (75.6%) located within the core range contained identifiable remains of *Cryptobranchus*, usually in the form of vertebrae; however, none of the faunal assemblages from the 11 Susquehanna watershed sites included any remains identified as *Cryptobranchus*.

We located 19 archaeological and 10 paleontological sites with identified amphibian remains in areas outside the known range of hellbenders (Fig. 2). Seven of these sites (24.1%) included hellbender remains. Five sites within the Potomac River watershed in Virginia and West Virginia contained Pleistocene fossils of *C. alleganiensis* (previously identified as *C. guildayi*) (Hubbard and Grady 2001; Bredehoeft 2010), one site in the lower reaches of the Mississippi River in the state of Mississippi contained bones from one specimen of *C. alleganiensis* (Kassabaum 2014), and one site in the Mobile River watershed in Alabama contained two bone fragments identified as hellbender (Lovett 2010).

Historical range descriptions.—We obtained 77 historical natural history sources (Supplemental Information Part 3) describing the general range of the hellbender with publication dates between 1800 and

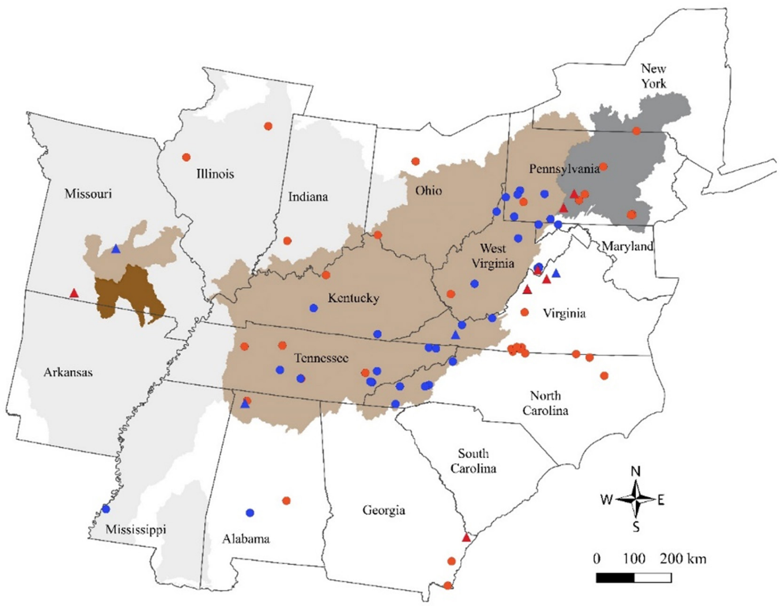

Figure 2. Map of 81 archaeological and paleontological sites with identified amphibian assemblages in U.S. states surrounding the modern range of Eastern Hellbenders (*Cryptobranchus alleganiensis*). Blue markers indicate locations where *C. alleganiensis* remains were found and red markers indicate locations where *C. alleganiensis* remains were absent. Triangles represent paleontological sites and circles represent archaeological sites. The Susquehanna River watershed is shown in dark gray, the core range in light brown, and the range of the Ozark hellbender subspecies (*C. a. bisopi*) in dark brown. Light gray shading indicates areas within the Mississippi watershed, but not within the known range of *C. alleganiensis*. Hellbender remains were present at 75.6% of sites within the core range and 24.1% of sites outside the known range of the species. Hellbender remains were absent from all 11 sites within the Susquehanna watershed. Site details and sources can be found in Supplemental Information Part 1.

1974 (Table 1; note that one source contained separate records for two time-intervals). No source referred to hellbenders as being absent or rare from the core range, indicating general acceptance of the presence of this species in these areas since the earliest reports. For the Susquehanna River Basin, however, a pattern of increasing recognition of hellbender presence over time was apparent. Of the three pre-1825 sources, none recognized the hellbender as an inhabitant of the Susquehanna, and two sources described the species as being absent in that watershed. Fewer than 50% of sources prior to 1900 recognized the hellbender as a Susquehanna species, and some sources continued to describe them as rare in that watershed until 1950.

Location-specific occurrence records.—We obtained 296 location-specific reports of hellbender sightings from approximately 1650–1999 in New York, Pennsylvania, and Maryland (Fig. 3, Table 2). Reports prior to 1800 were all from the Ohio River watershed and

Table 1. Eastern Hellbender (*Cryptobranchus alleganiensis*) presence or absence in core range and disjunct Susquehanna watershed of the USA as provided by historical sources from 1800 to 1974. A single source may contain information about both the core range and disjunct Susquehanna watershed. Abbreviations and identifiers are n = number of sources per time interval, Present = reported within that range, Absent = reported to be absent from that range, Rare = reported as present, but with a qualifier such as rarely seen or uncommon.

		Core Range			Susquehanna		
	n	Present	Rare	Absent	Present	Rare	Absent
1800–1824	3	3	0	0	0	0	2
1825–1849	8	7	0	0	1	1	0
1850–1874	7	6	0	0	2	1	0
1875–1899	27	25	0	0	2	1	1
1900–1924	19	16	0	0	3	2	0
1925–1949	8	6	0	0	3	2	0
1950–1974	6	6	0	0	4	0	0
Total	78	69	0	0	15	7	3

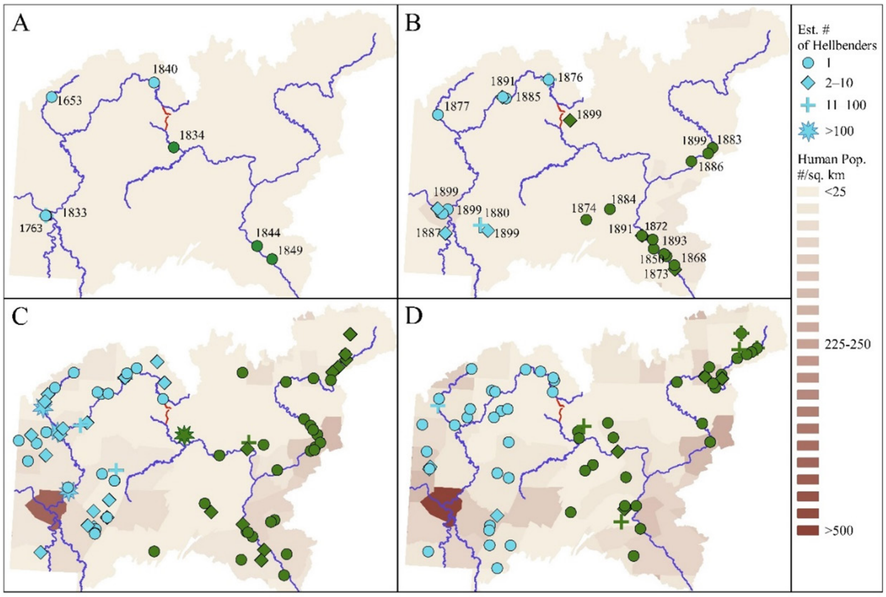

Figure 3. Location and estimated number of Eastern Hellbenders (*Cryptobranchus alleganiensis*) in the USA reported in historic documents from (A) < 1800–1849 (n = 9), (B) 1850–1899 (n = 43), (C) 1900–1949 (n = 124), and (D) 1950–1999 (n = 120). Main rivers are indicated in blue and hypothesized location of hellbender entry to the Susquehanna watershed through drainage rearrangement is shown in red. Locations within the core range are shown in light blue and those within the disjunct Susquehanna watershed are shown in green. Background color indicates human population density (https://geo.nyu.edu/). Report dates are indicated in panels A and B to illustrate the timing of initial spread of sightings throughout the Susquehanna watershed. If multiple sightings were made in the same location, only the year of the earliest sighting is displayed.

pre-date the formal description of the species (Sonnini and Latreille 1801; Michaux 1805) and its subsequent scientific naming (Daudin 1803). The oldest report, dating to approximately 1653, refers to the observation of a single unknown aquatic animal on an Allegheny River tributary, described as a "snake" with a dark-colored, 2-foot-long body, wide head, four feet and legs, small nose at the tip of the head, and a tail. Although it cannot be certain this description was of a hellbender, no other animal known to be found in the watershed fits this description well (Wykoff 1995). A second pre-1800 sighting was reported by renowned naturalist John Bartram at the Ohio River in Pittsburg, Pennsylvania in 1763. He described it as a "small alligator" with a "flat proboscis" and believed it to be a new genus of "water lizard" (Darlington 1849).

Later reports of hellbenders were more specific in terms of species identification. Most included photos or detailed descriptions sufficient to distinguish hellbenders from other species, such as the Common Mudpuppy (*Necturus maculosus*), with which it is often confused. From 1800–1849 (Fig. 3), two additional encounters were reported in the core range: approximately 12 animals captured in a relatively uninhabited portion of the Allegheny region of New York and 34 hellbenders taken near Pittsburgh, Pennsylvania, USA.

In contrast to the core range sightings in the Ohio River watershed, the earliest report of a hellbender in the Susquehanna watershed dates to 1834, when one was captured in the Sinnemahoning subbasin of the Susquehanna watershed. Two additional sightings were reported from the lower reaches of the Susquehanna

Table 2. Summary of Eastern Hellbenders (*Cryptobranchus alleganiensis*) from the USA reported in 296 historical hellbender sightings, by watershed and 50-y time interval. The acronym CR = stream systems within the core range portion of the study area, including the Allegheny, Ohio, and Monongahela River watersheds and SUS = Susquehanna River watershed. Values for highest single report reflect reported numbers only (estimated values were excluded).

	< 1800–1849		1850–1899		1900–1949		1950–1999	
	CR	SUS	CR	SUS	CR	SUS	CR	SUS
Number of Reports	6	3	17	26	71	53	61	59
Estimated Number of Animals	48	3	324	213	2290	538	542	340
Average Animals/Report	8.00	1.00	19.06	8.19	32.25	10.15	8.89	5.76
Highest Single Report	34	1	100	165	750	250	152	52

approximately 10 y later, in 1844 and 1849. Each of the reports described only a single hellbender observed.

During each successive 50-y time interval, reports of hellbenders became more numerous and widespread. The pattern of sightings, however, appears to differ considerably between Susquehanna and the core range, both in the distribution of sightings and numbers of animals reported (Fig. 3). Core range reports often indicated multiple animals captured together, frequently in the context of scientific collection. Hellbender sightings extended throughout the Allegheny, Ohio, and Monongahela subbasins, with the largest concentrations of reports coming from areas with the highest human populations. In the Susquehanna watershed, nearly all hellbender reports before 1900 occurred in the lower reaches of the Susquehanna River and on the West Branch, and all indicate observation of only a single animal. Only three hellbender occurrences were reported on the North Branch Susquehanna River before 1900, and hellbenders were not reported from the uppermost reaches of the watershed in New York until the 1920s despite areas with relatively high human populations prior to that time.

For all 50-y time intervals, the estimated number of hellbenders reported and average number of hellbenders per report were higher for streams in the core range (Table 2). For all time intervals except 1850–1899, these streams also had a greater number of reports and exceeded Susquehanna basin streams in the maximum number of animals reported in a single event. During the late 1800s, several sources reported large numbers of hellbenders taken together, usually on catfish lines, in the West Branch Susquehanna and its tributaries. The number of animals reported from 1850–1899, however, was still highest in the core range portion of the study area with 324 individuals, compared to 213 reported from the Susquehanna.

Discussion

The historical evidence we examined supports the hypothesis that hellbenders are a recent arrival to the Susquehanna River watershed. Archaeological and paleontological records failed to reveal any known occurrences of remains of *Cryptobranchus* within the watershed. Natural history sources indicate that prior to the mid-1800s, hellbenders were generally not considered to be part of the Susquehanna River fauna, and location-specific occurrence reports of hellbender sightings illustrate a clear pattern of spread through the Susquehanna watershed over time. Although historical records cannot determine with certainty whether hellbenders moved into the Susquehanna through natural or anthropogenic means, further consideration of these results within the context of the history of the region may provide insight into the origins of hellbender populations in the Susquehanna watershed.

Prehistoric hellbender range**—**Fossil specimens and archaeological remains provide the earliest available evidence of the distribution of hellbenders. Although the absence of *Cryptobranchus* from the identified faunal remains does not definitively indicate prehistoric absence from the Susquehanna watershed, it seems unlikely that *Cryptobranchus* remains would have been fully destroyed or overlooked in all 11 Susquehanna locations. Remains at several of these sites were examined by paleontologist John Guilday (Guilday and Bender 1958; Guilday et al. 1962, 1964; Guilday and Parmalee 1965), who identified *Cryptobranchus* bones at numerous sites throughout the core range.

Archaeological and paleontological evidence also suggest that the prehistoric range of hellbenders may have included areas from which the species has not been observed in modern times. Remains of *Cryptobranchus* sp. were present in five of seven Pleistocene faunal assemblages from the Potomac River watershed (Hubbard and Grady 2001; Bredehoeft 2010). Single specimens were also reported from one site in the Lower Mississippi (Kassabaum 2014) and another in the Alabama River subbasin of the Mobile Bay watershed (Lovett 2010). Although these two specimens could be the result of trade among indigenous people rather than an indication of a larger historical range, it is notable that a modern survey in Georgia discovered hellbenders in a tributary of the Alabama River (Albanese et al. 2011). The existence of evidence of *Cryptobranchus* remains in these sites further underscores their notable absence from the Susquehanna region.

Archival records illustrate historical hellbender expansion.**—**The archival records we examined provide further support for a recent introduction of hellbenders to the Susquehanna watershed. Natural history accounts indicate that hellbenders were not universally considered part of the Susquehanna River fauna until the early 1920s, and sources published in the northern reaches of the watershed continued to refer to it as rare until nearly 1950. The suggestion that hellbenders were a new arrival to the Susquehanna was a common theme, particularly among official sources from Pennsylvania state agencies. The Pennsylvania Department of Fisheries (1906) stated that the species was believed to live only "west of the Alleghenies." A later report by the Pennsylvania Board of Fish Commissioners (1938) stated that hellbenders occurred in streams of the Ohio watershed, and that it had also "reached the Susquehanna drainage." Newspaper articles advertised hellbenders captured in the Susquehanna River on display as "oddities" in private homes or businesses, sometimes suggesting that the animal must have escaped from a zoological collection. In contrast, accounts from within the core range suggest that the public had a higher familiarity with hellbenders in those regions.

Written accounts by early North American naturalists and explorers further support the absence or rarity of hellbenders from the Susquehanna watershed. Several prominent explorers traveling within the core range mention hellbenders in their logs and memoirs (Bartram 1763 [in Darlington 1849]; Michaux 1805; Barton 1812; Trego 1843; Maximilian 1906), and by the mid-1800s large numbers of hellbenders were being taken for scientific research and sale from locations within the Ohio watershed (Smithsonian 1876). Early explorers of the Susquehanna watershed, however, did not report hellbenders in their accounts. Bartram himself had conducted natural history surveys of the Susquehanna River system in 1743 (Hoffman and Van Horne 2004) yet described the hellbender as a new discovery when he encountered it in Pittsburgh (within the Ohio River watershed) years later.

Individual hellbender occurrence reports suggest a pattern of spread through the Susquehanna River watershed that contrasts notably with the spatial and temporal distribution of sightings in the core range. Hellbenders were found throughout the core range in all time intervals, with the earliest sightings located near human population centers, such as Pittsburgh, Pennsylvania, and Olean, New York. This suggests that the pattern of sightings in the core range primarily reflects the distribution of the human population. By contrast, the pattern of occurrence reports in the Susquehanna appears to closely follow a pattern of spread along the river system. Despite the presence of human population centers such as Binghamton, New York, and Harrisburg, Pennsylvania, we located no Susquehanna account predating the early 1830s, when one hellbender was reported from a rural area of Sinnemahoning Creek, several kilometers downstream of the divide between the Susquehanna and Ohio river watersheds. Approximately 10 y later, hellbenders were reported from the lower reaches of the Susquehanna River near Harrisburg, Pennsylvania, and in 1854 specimens were collected from the mouth of the river at Chesapeake Bay. By 1890, Harrisburg, Pennsylvania, with a human population of approximately 39,000 (https://www.census.gov/population/www/documentation/twps0027/tab12.txt), had become a hotspot for hellbender sightings, while Binghamton, New York, with just over 35,000 people, had no published sightings of hellbenders, and Scranton, Pennsylvania (along the North Branch), with a population of over 75,000 people, reported only three animals. At approximately the same time, reports of extremely high abundance of hellbenders were becoming common along the West Branch Susquehanna and its tributaries, largely from areas with sparse human populations. No reports of hellbenders in the uppermost reaches of the Susquehanna watershed in New York State were found prior to 1920, suggesting a slow upstream spread to the northernmost reaches of the watershed.

Possible routes and mechanisms of movement—The distribution of the earliest sightings of hellbenders in the Susquehanna River watershed suggests two points of entry: Sinnemahoning Creek and the lower reaches of the Susquehanna River near Chesapeake Bay. The first known report of a hellbender occurred on Sinnemahoning Creek in approximately 1834; however, records from the Chesapeake Bay area began to appear just 10 y later. Natural downstream movement to the Chesapeake Bay area from Sinnemahoning Creek would have required traversing nearly 250 km of river in 10 y. Hellbenders reportedly have low vagility and small home ranges (Peterson 1987; Humphries and Pauley 2005; Burgmeier et al. 2011a). Although many stream salamanders are known to disperse in downstream currents (Johnson and Goldberg 1975; Stoneburner 1978; Thiesmeier and Schuhmacher 1990) or be swept downstream during floods (Zhang et al. 2016), these movements are typically much shorter. Because rapid dispersal of hellbenders either up or down the length of the Susquehanna seems unlikely, this suggests two distinct colonization events, and possibly two mechanisms of introduction.

Sinnemahoning Creek is located along the divide between the Ohio and Susquehanna watersheds, where it closely approaches streams of the Allegheny River headwaters. Despite a lack of flood records for this region predating the early 1900s, modern records indicate that large flooding events are relatively common. Notable events with catastrophic flooding occurred in the region in 1911, 1936, 1942, and 1972 (Grover 1937; Eisenlohr 1952; Neely and George 2006). This region has also been the hypothesized point of entry to the Susquehanna via stream capture for a variety of species. Netting (1932) proposed that Blanding's Turtles (*Emydoidea blandingii*) and Map Turtles (*Graptemys geographica*) may both have travelled to the Susquehanna along with the hellbender in a stream capture event. Ortmann (1913) suggested this region as the likely point of entry, also via stream capture, of a mussel species belonging to the genus *Strophitus*. Greenside Darters (*Ethyostoma blennioides*) were first found in the Susquehanna within the Sinnemahoning Creek subbasin in the 1960s. Examination of meristic data from Greenside Darters in the Allegheny, Genesee, and Susquehanna watersheds led Denoncourt et al. (1977) to conclude that the species had migrated to the Susquehanna from the Allegheny drainage via stream capture in Holocene times. Genetic studies of Greenside Darters show similar patterns to those seen in hellbenders, with Susquehanna specimens grouping closely with those from the Ohio River watershed, and few unique Susquehanna haplotypes (Haponski and Stepien 2008). Although the exact location of any species dispersing across the divide between the Allegheny and Susquehanna basins cannot be definitively determined, the Sinnemahoning region appears to be an excellent candidate.

Despite the plausibility of a stream capture event or other form of drainage rearrangement, anthropogenic introduction cannot be discounted as a potential mechanism of movement, particularly for hellbenders first appearing in the lower reaches of the Susquehanna River. Although hellbenders are not generally thought of as having any substantial economic value, historically there was demand for them both as scientific and educational specimens and as a food item. The earliest record of large-scale scientific collection of hellbenders reported 100 animals taken from the Allegheny River in 1876 (Grote 1876); however, scientific collection and subsequent shipping of hellbenders from locations in the core range was occurring even before hellbenders were formally known to western science. In 1763, Bartram referred to the loss of a specimen of his Pittsburgh "alligator" that had been sent off for study (Darlington 1849). Hellbenders from Pittsburgh were also sent to Harlan (1825) at the Philadelphia Museum and were listed in the specimen records of the Catalogue of Amphibian Specimens of the British Museum in 1850 (British Museum 1850). Maximilian, Prince of Wied, recounted taking 34 specimens for study from the Pittsburgh area in 1833 (Maximilian 1906). Annual reports made by the Board of Regents of the Smithsonian Institution included hellbenders among their yearly specimen acquisitions, always from locations within the core range (Smithsonian Institution 1855, 1876).

Many accounts of hellbender transport in the 1800s indicate that animals were shipped live, both across the country and internationally. Townsend (1882) described carrying live specimens captured in western Pennsylvania six miles on horseback. Live hellbenders were sent to locations in Europe and the U.S., and two major sources appear to have supplied the hellbender trade: the Smithsonian Institution in Washington, D.C., and the Fulton Fish Market in New York City. Smithsonian annual reports indicate that "large numbers" of hellbenders were sought for dissection and distribution (Smithsonian Institution 1856) and that specimens were shipped to museums, colleges, and zoological gardens in Europe (Smithsonian Institution 1868; Sclater 1879). The Fulton Fish Market in New York, known as one of the premier suppliers of freshwater and marine organisms in the 1800s, was a regular provider of hellbenders to the Smithsonian (White 1893), and directly shipped hellbenders to international customers (City of Liverpool 1889).

The most likely route of transport from the Ohio Watershed to the Smithsonian provides insights into the potential for anthropogenic introduction. Although the Erie Canal began operation in 1825 (Shaw 1966), the Allegheny Portage Railroad, which allowed people, boats, and goods to be transported over the divide between the Allegheny headwaters and Sinnemahoning Creek, would have provided a more direct route. The railway was in service from 1834 until it was replaced in the 1850s by rail service between Pittsburgh, Pennsylvania, and cities to the east (Baumgartner and Hoenstine 1952). Prior to the construction of the Portage Railroad, travel between the watersheds was still undertaken, usually by carrying canoes and goods and traversing over the ridgeline on foot (Maclay 1887; Leeson 1890). Animals transported via this route would likely have been taken down the Susquehanna River and shipped out from Chesapeake Bay, providing a mechanism for an introduction in that region.

Implications for conservation and management—Decisions regarding the management of potentially introduced disjunct populations are complex, particularly for species that are declining in their core range. Although introduced species often have negative consequences for native ecosystems, the magnitude and type of impact may vary. Some introduced species may be relatively benign in their effects on local biodiversity, while others may produce a combination of both negative and positive impacts (Schlaepfer et al. 2011; Vimercati et al. 2022). Management decisions regarding such species must be made from a balanced perspective, considering both the short-term and long-term impacts (Vitule et al. 2012). For declining species, disjunct populations may represent important reservoirs of genetic diversity, or strongholds for species that may be lost within their core range. For example, Reilly et al. (2014) make a case for the conservation of a disjunct population of Red-bellied Newts (*Taricha rivularis*) due to its importance for the long-term survival of the species, despite being unable to determine whether the population was naturally occurring or anthropogenically introduced. Furthermore, species that have been present for some time, even if nonnative, may be integrated into local cultural values, and in some cases public support may be higher for the introduced species than for other native taxa (Clavero 2014), although this may not be a reason to keep these species if conservation of native species is threatened.

In the case of Susquehanna hellbenders, there is little information to assess their impacts on the ecosystem, and significant uncertainty about the mechanism of their arrival. Hellbenders populations within the Susquehanna River system appear to have experienced considerable declines in recent decades (Quinn et al. 2013; Foster 2018), and conservation efforts have focused heavily on stabilizing the few remaining populations through habitat augmentation and the release of head-started individuals (Peter Petokas, pers. comm.). Hellbenders are a culturally significant species, as evidenced by their recent approval as the Pennsylvania state amphibian (https://www.governor.pa.gov/newsroom/pennsylvania-declares-eastern-hellbender-as-official-state-amphibian/) and their frequent mention in historical sources. They may function as an iconic or flagship species, serving as a focal point for communicating with the public about regional conservation issues (Horsley et al. 2020). They may also play an important role in Susquehanna ecosystems, particularly in regard to controlling the invasive Rusty Crayfish (*Faxonius rusticus*). Although Cava et al. (2018) indicated that captive-reared hellbenders showed a preference for native crayfish species, both the Cava study and that of Hartzell et al. (2022) demonstrated that hellbenders can prey on Rusty Crayfish.

Given the documentation of range-wide declines of hellbenders within their core range (Wheeler et al. 2003; Foster et al. 2009; Burgmeier et al. 2011b), the significance of the Susquehanna watershed as the northernmost edge of the hellbender range, and the genetic distinctness of Susquehanna hellbender populations (Rayman 2010; Unger et al. 2013), hellbenders in the Susquehanna River watershed may represent an important reservoir for the species in the face of ongoing habitat loss and climate change. Climatic modeling studies have projected that hellbenders could lose up to 61% of their climatic niche by 2050 (Sutton et al. 2015), and that most of this loss will occur in the southern portions of the core range (Roark 2016). Further study on the role of hellbenders in Susquehanna ecosystems, their impacts on local biodiversity, and their adaptations to unique local conditions may provide important insights on the conservation value of populations in Susquehanna River system, regardless of their mechanism of arrival. Understanding the history of these populations and their relationships to hellbenders in other portions of the range adds an important new dimension to discussions of how to best manage hellbenders throughout the Susquehanna River basin.

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Robin L. Foster is an Assistant Professor in the Department of Animal Behavior, Ecology, and Conservation at Canisius College in Buffalo, New York, USA. She received her B.A. in Education from Canisius (1996) and her B.A. (2004) and M.A. (2006) in Biology from the State University of New York, Buffalo State University, USA. Robin completed her Ph.D. in Evolution, Ecology, and Behavior at the University at Buffalo, New York, USA, where she studied the current and historical distribution of Eastern Hellbenders (*Cryptobranchus alleganiensis*) in the Susquehanna River watershed. Her research interests center on the use of minimally invasive methods for wildlife population monitoring and herpetological conservation, including environmental DNA, remote photo and video techniques, and historical ecology. (Photographed by Malini Suchak).

Chris P.S. Larsen is a Professor in the Department of Geography at the University at Buffalo, State University of New York, in Buffalo, New York, USA, where he also serves as the Director of Graduate Studies for the Department of Environment and Sustainability. His research interests include wildfire, historical ecology, and anthropogenic impacts on plant communities. (Photographed by Wendy Scheers).

Amy M. McMillan received a B.S. in Zoology at North Dakota State University, Fargo, North Dakota, USA, and a M.A. in Systematics and Ecology, and Ph.D. in Entomology at the University of Kansas, Lawrence, Kansas, USA. A Professor at Buffalo State University, Buffalo, New York, USA, Amy is broadly interested in species of conservation concern and the evolutionary consequences of anthropogenic environmental impacts on those species. Her work with hellbenders has included demographics, behavior, population genetics, education, and disease. Currently, she directs the Honors Program at Buffalo State University. (Photographed by Jesse Steffan-Colucci).