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Attributes of Shelters Selected by Eastern Hellbenders (*Cryptobranchus a. alleganiensis*) in the French Broad River Basin of North Carolina

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Abstract.—**We investigated the attributes of shelters used by Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) in two 500-m stretches of the French Broad River basin in North Carolina during June 2010. We quantified attributes at each Hellbender shelter and at a corresponding unoccupied shelter located <25 m away to determine whether the attributes selected differed from those available in the surrounding environment. We identified 41 Hellbender shelters, each occupied by a single animal. Hellbenders selected shelters that had larger cover rocks and deeper cavities than the unoccupied shelters. No other attributes differed between occupied and unoccupied shelters, and there were no significant relationships between total length of Hellbenders and size of the cover rock or cavity depth. All Hellbender shelters were formed by large rocks with flat bottoms. Most had a single entrance that was oriented downstream and a cavity floor consisting of sand and gravel. Shelters were generally located in shallow, fast-flowing water with <10% of their surface area embedded in the substrate. Our results suggest that Hellbenders prefer shelters with attributes that maximize cavity space. Larger cavities likely provide greater protection from predators and greater concealment from sunlight. In addition, larger cavities allow more space for Hellbenders to rock back and forth to maximize oxygen uptake through their skin during periods of low flow when oxygen levels drop.**

Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) are large, aquatic salamanders restricted to the eastern United States (Petranka, 1998). They are habitat specialists requiring highly-oxygenated, fast-flowing waters with large rocks and an abundance of prey (Smith, 1907; Nickerson and Mays, 1973; Williams et al., 1981; Humphries and Pauley, 2005). Hellbenders range throughout the central and southern Appalachian Mountains from southern New York to northern Alabama and portions of the Ozark Mountains in Missouri and northern Arkansas (Petranka, 1998). Hellbenders were once thought to be common prior to European colonization (Petranka, 1998). However, during the past century they have declined substantially throughout their range because of a variety of factors including stream impoundment, pollution, and siltation (Nickerson and Mays, 1973; Williams et al., 1981; Wheeler et al., 2003; Foster et al., 2009), overharvesting (Nickerson and Briggler, 2007), and possibly the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*; Briggler et al., 2008). Currently, Hellbenders are listed as a Federal Species of Concern, with a global rank of G3/G4, and in North Carolina as a Species of Special Concern with a state rank of S3 (LeGrand et al., 2010).

Large, flat rocks are an essential component of Hellbender habitat (Smith, 1907; Hillis and Bellis, 1971; Nickerson and Mays, 1973; Humphries and Pauley, 2005). Both males and females use these rocks because they provide structure for shelters (Smith, 1907; Nickerson and Mays, 1973; Humphries and Pauley, 2005). Shelters are occupied year-round and conceal the occupants from daylight and provide protection from predators (Smith, 1907; Nickerson and Mays, 1973). The male's shelter also serves as a nest site where egg deposition, fertilization, and brooding occur (Smith, 1907; Bishop, 1941; Nickerson and Mays, 1973). Hellbenders defend their shelters and rarely share them with other individuals (Smith, 1907; Hillis and Bellis, 1971; Nickerson and Mays, 1973; Humphries and Pauley, 2005).

To date, no comprehensive study of Hellbender shelters has been conducted. Most information characterizing shelters is qualitative, with the exception of two atypical shelters in the North Fork of the White River in Missouri described by Nickerson and Tohulka (1986) and the dimensions of cover rocks that form the shelters (e.g., Smith, 1907; Hillis and Bellis, 1971; Nickerson and Mays, 1973; Humphries and Pauley, 2005). In addition, no studies have compared the attributes of shelters used by Hellbenders to those available in the surrounding habitat. As a result, only limited inferences can be made about the relative importance of shelter attributes preferred by Hellbenders. In this study, we quantify the attributes of shelters used by Hellbenders and determine whether the attributes selected differ from those available in the surrounding environment.

Materials and Methods

We conducted our study during June 2010 in two 500-m stretches of river in the French Broad River Basin in North Carolina (elevation 655–750 m). The study sites are part of the Muscovite-biotite gneiss unit of the Ashe Metamorphic Suite and Tallulah Falls Formation in the Blue Ridge Belt (North Carolina Geologic Survey, 1985). We selected these sites because they represent two potentially different types of habitats used by Hellbenders (L. Williams, pers. comm.). The first stretch of river represented an upper reach with protected headwaters and intact forested riparian habitat. The second stretch represented a middle reach, located ca. 12 river-km downstream, that flowed through a mix of residential and agricultural lands. The riparian habitat was narrow and partially forested with some undercut and eroding banks. This stretch was generally deeper than the first and received higher sediment loads during precipitation events.

We located Hellbender shelters by using a log peavey to lift rocks and search for Hellbenders. We sampled each stretch of river starting at the downstream end and minimized disturbance by slowly lifting rocks on the downstream side and parallel to the current and then slowly placing them back in the same position as found. When a Hellbender was discovered, it was caught by hand and transferred to a dip net for processing. We marked each shelter with a weighted float to facilitate

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TABLE 1. Sampling procedures used for measuring attributes of Hellbender shelters.

Attribute	Method
Cover rock area	Calculated by multiplying the maximum straight-line width of the cover rock by the perpendicular, maximum straight-line length, measured using a meter stick
Cover rock shape	Categorized as either flat, round, or round with flat bottom
Percent embeddedness	Visual estimate of the proportion of the cover rock buried in the substrate
Number of entrances	Count of the number of openings around the cover rock large enough for a Hellbender to use as a shelter entrance
Entrance orientation	Absolute difference between the bearing of the entrance and downstream direction; compass was held 1 m above the center of the shelter and oriented 0 degrees downstream
Range of entrance orientation	Used as a proxy for entrance length; calculated by taking the difference of compass bearings measured in the direction of each entrance endpoint, using the same method as described for entrance orientation
Mean entrance height	Measured from the top of the substrate to the bottom of the cover rock using a meter stick; calculated using measurements at three equidistant points along an entrance
Maximum entrance height	Measured from the top of the substrate to the bottom of the cover rock at the point where the entrance was the largest
Mean cavity depth	Measured from the perpendicular edge of an entrance to the back of a shelter using a meter stick; calculated using measurements at three equidistant points along an entrance
Maximum cavity depth	Measured from the perpendicular edge of an entrance to the back of the shelter at the point where the cavity depth was greatest
Cavity substrate	Visual classification of the dominant substrate of the cavity floor, recorded as one of five types: sand (0.10–2 mm), gravel (2–65 mm), cobble (65–250 mm), bedrock, or detritus (modified from Rosgen, 1996).
Stream depth	Measured at the deepest point around a shelter using a meter stick
Flow rate	Measured on the upstream side of the shelter at 60% water depth using a Global Flow Probe FP101, Global Water Instrumentation, Inc., Gold Rover, CA

relocation. For each Hellbender captured, we determined the sex and age (adult or juvenile) based on size and presence of a swollen ring around the cloaca of males (Smith, 1907), and we measured the total length (TL) to the nearest 0.5 cm using a halved PVC pipe with a measuring tape affixed to it. Once processing was completed, we released each Hellbender at the capture site.

We used a mask and snorkel to collect attribute data on each shelter within 1 to 7 days of locating them. Shelter attributes included size and shape of the cover rock, percent of cover rock embedded in the substrate (percent embeddedness), number of entrances, mean and maximum entrance height, entrance orientation, range of entrance orientation (used as a proxy for entrance length), mean and maximum cavity depth, and cavity substrate. We also measured stream depth and flow rate at each shelter (see Table 1 for sampling procedures).

To determine whether the attributes of occupied shelters differed from those available in the surrounding environment, we identified a corresponding unoccupied shelter <25 m from each occupied shelter. We used a random-numbers table to determine the direction (0–360°) that an unoccupied shelter was located from an occupied shelter. An unoccupied shelter was considered suitable if it had a cover rock with a straight-line diameter >38 cm (Hillis and Bellis, 1971) and had no Hellbenders present. We searched along the random direction until a suitable unoccupied shelter was found. In the event that there was no suitable shelter along the random direction, we generated a new random direction and repeated the procedure until a suitable shelter was located. Once an unoccupied shelter was selected, the rock was lifted in the same manner as an occupied shelter and checked for Hellbenders. We measured attributes of unoccupied shelters on the same day as the corresponding occupied shelters.

We used a mixed linear model to determine if there was a difference between attributes of occupied and unoccupied shelters for all variables except shape of cover rock. The form of the model was: response difference of attribute between occupied and unoccupied shelters = intercept + study site effect + random error. Study site effect was considered a random effect and differences between occupied and unoccupied shelters were considered significant if the intercept was significantly different from 0. Because size of cover rock and stream flow exhibited positively skewed residuals in the original analysis, we used a logarithmic transformation on the variables before taking the difference between occupied and unoccupied shelters and applying the mixed model. We used a McNemar's test to compare the shape of the rocks. If a shelter had more than one entrance, only data from the largest entrance were used in the analysis. We also excluded pairs from the analysis if data were missing or if unoccupied shelters did not have an entrance. To determine if size of cover rock or maximum cavity depth was related to size of the Hellbender, we used a mixed linear model with size of cover rock and maximum cavity depth as predictor variables and site as a random effect fit to TL of the Hellbender as the response variable. We transformed size of cover rock using the natural log to reduce the influence of outliers. An examination of residuals from the model did not reveal nonnormality or unequal variances. We used Spearman correlations (r_s) to examine the association between log rock size and maximum cavity depth for both occupied and unoccupied sites. We used SAS version 9.2 for all statistical analyses and considered results significant at alpha <0.05.

RESULTS

We located 41shelters (23 in the upper stretch, 18 in the lower stretch). Each shelter was occupied by only one animal. We were unable to collect data on four shelters in the lower stretch of river because of vandalized location markers. We captured 23 Hellbenders (six adult males, nine adult females, and eight juveniles) and 18 animals escaped (10 in the upper stretch, 8 in the lower stretch). We did not include temporary cover rocks used by escaped animals in our analysis because animals always fled downstream to areas surveyed previously. Mean TL

TABLE 2. Descriptive statistics comparing attributes of corresponding occupied and unoccupied Hellbender shelters in two sections of river in the French Broad River basin, North Carolina, June 2010.

		Occupied shelters			Unoccupied shelters			
Attribute	*N*[a]	Median	Q1[b]	Q3[b]	Median	Q1	Q3	*P*-value[c]
Cover rock area (cm^2)	37	4,582	3,124	6,480	2,478	2,135	3,162	0.0002
Percent embeddedness (%)	34	2	1	5	2	1	10	0.13
Mean entrance height (cm)	34	7.7	5.7	11.3	9.0	5.0	10.7	0.93
Maximum entrance height (cm)	29	11.0	8.0	15.0	11.0	7.0	13.0	0.15
Entrance orientation (°)	28	60	20	80	29	10	60	0.09
Range of entrance orientation (°)	27	95	60	140	90	60	130	0.83
Mean cavity depth (cm)	29	36.3	27.0	48.7	18.7	14.3	24.3	<0.0001
Maximum cavity depth (cm)	29	49.5	38.0	64.0	29.5	21.5	43.0	0.0001
Stream depth (cm)	36	51.0	31.0	62.0	42.0	30.5	59.5	0.41
Flow rate (ms^{-1})	37	1.9	1.4	3.0	1.6	1.2	2.8	0.38

[a] *N* denotes the number of corresponding pairs of occupied and unoccupied shelters used in the analysis.
[b] Q1, lower quartile; Q3, upper quartile.
[c] A mixed linear model was used to compare attributes of corresponding pairs of occupied and unoccupied shelters.

was 37.7 cm (SE = 2.0) for males, 38.4 cm (SE = 1.2) for females, and 25.1 cm (SE = 2.3) for juveniles. There were no significant relationships between size of cover rocks or maximum cavity depths and TL of Hellbenders (all $P > 0.46$).

Occupied shelters had significantly larger cover rocks than did unoccupied shelters ($P = 0.0002$; Table 2). Shape of cover rocks did not differ between occupied and unoccupied shelters ($P = 0.37$). Cover rocks were either flat (occupied: $N = 25$, 68%; unoccupied: $N = 21$, 57%) or round with flat bottoms (occupied: $N = 12$, 32%; unoccupied: $N = 16$, 43%); no cover rocks were round. Percent embeddedness of cover rocks was relatively small and did not differ between occupied and unoccupied shelters (median = 2% for both occupied and unoccupied shelters; $P = 0.13$; Table 2). The majority of occupied ($N = 32$, 86%) and unoccupied ($N = 35$, 95%) shelters had only one entrance; the others had two entrances. Entrances were generally oriented downstream, and their orientation did not differ between occupied and unoccupied shelters ($P = 0.09$). Range of entrance orientations (used as a proxy for entrance length) and entrance heights also did not differ between occupied and unoccupied shelters (both $P > 0.15$; Table 2). Occupied shelters had significantly greater mean and maximum cavity depths than did unoccupied shelters ($P < 0.0001$; $P = 0.0001$; Table 2), and maximum cavity depth was correlated with size of cover rock for both occupied ($r_s = 0.49$, $P = 0.003$) and unoccupied shelters ($r_s = 0.44$, $P = 0.01$). Cavity substrate was similar for occupied and unoccupied shelters and consisted primarily of sand and gravel (Fig. 1). There were no differences in stream depths and flow rates at occupied and unoccupied shelters (both $P > 0.39$; Table 2). The effect of location on the difference between occupied and unoccupied shelters was estimated to be 0 for all of the variables except for stream flow, which had a small estimated variance in the differences due to location (location variance = 0.22, residual variance = 2.18).

DISCUSSION

Many authors have suggested that Hellbenders prefer shelters consisting of large rocks (e.g., Smith, 1907; Nickerson and Mays, 1973; Hillis and Bellis, 1971; Humphries and Pauley 2005). Our finding that Hellbenders occupied shelters with larger cover rocks than those at unoccupied shelters verifies this assertion and indicates that the size of a cover rock is an important attribute determining the suitability of a shelter. Median cover size of rocks of occupied shelters was 46% larger than that of unoccupied shelters (Table 2). This difference was likely conservative, as we were unable to sample many of the largest rocks in the river because they required more than two peavey bars to lift them. These data, along with observations made during the study, suggest that Hellbenders preferred shelters formed by the largest rocks in the river. Hellbenders likely select larger rocks because they provide greater protection from sunlight and predators (Smith, 1907; Nickerson and Mays, 1973) as well as providing more cavity space.

The importance of flat rocks to Hellbenders has also been noted by many authors (e.g., Bishop, 1941; Dundee and Dundee, 1965; Gates et al., 1985; Nickerson et al. 2003). In our study, all occupied shelters had cover rocks with relatively flat or concave bottoms, suggesting that the rock's underside is an important feature that helps define the space of the cavity. Hillis and Bellis (1971), who reported similar findings in Pennsylvania, suggested that Hellbenders did not choose round rocks because they were too embedded in the substrate and did not contain enough surface area for concealment. Nickerson et al. (2003) came to similar conclusions and further suggested that Hellbenders do not use round rocks because they allow too much light penetration around their margins.

Humphries and Pauley (2005) suggested that rocks partially embedded in the substrate could be an important attribute for

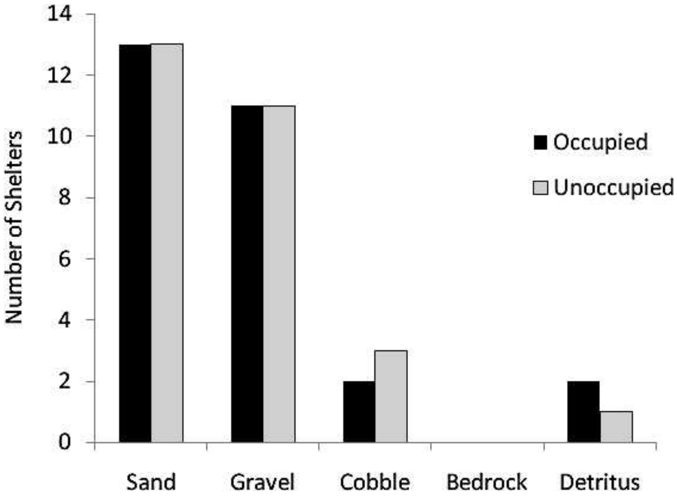

FIG. 1. Dominant substrate of cavity floors in 28 occupied and 28 unoccupied Hellbender shelters in two sections of river in the French Broad River basin, North Carolina, June 2010.

determining a rock's suitability as a shelter. Our results do not support this, as percent embeddedness did not differ between occupied and unoccupied shelters (Table 2). Additionally, cover rocks in our study were generally not deeply embedded in the substrate, which was composed primarily of sand and gravel and only small amounts of silt. Humphries and Pauley (2005) did not elaborate on the characteristics of embeddedness that make a rock suitable, but observations by Bishop (1941) indicated that shelters used for nesting were always at least partially embedded in the substrate to prevent eggs from washing downstream, whereas shelters used by nonbreeding individuals also included rocks lying loosely on the surface. Williams et al. (1981) surmised that cover rocks embedded by silt decreased the survival and reproductive success of Hellbenders, and Humphries and Pauley (2005) reported no captures in heavily silted areas. It is possible that our estimates of embeddedness were conservative because of the disturbance associated with lifting rocks. Future studies should consider investigating the characteristics of embeddedness in relation to the quality of a shelter.

Smith (1907) indicated that Hellbenders generally use natural openings as entrances to their shelters. However, in a few cases he observed entrances that were burrow-like and appeared to be excavated (Smith, 1907). Our results suggest that Hellbenders did not excavate entrances, as entrance heights and lengths did not differ between occupied and unoccupied shelters. This is to be expected, as enlarged entrances would potentially increase the amount of light penetration into the cavity as well as increase the risk of predation.

Hellbenders are known to use cover rocks with entrances that are generally oriented downstream (Smith, 1907; Alexander, 1927; Bishop, 1941; Humphries and Pauley, 2005), with two exceptions described by Nickerson and Tohulka (1986). Occupied shelters in our study were also oriented downstream. Humphries and Pauley (2005) speculated that rocks with entrances facing downstream could be an attribute that determines suitability for a shelter. Our finding that entrance orientation did not differ between occupied and unoccupied shelters does not support Humphries and Pauley's (2005) assertion. It does, however, indicate that most openings under rocks are naturally oriented downstream because any openings oriented upstream likely fill in with sediment during high flow events.

The finding that occupied shelters had greater cavity depths than unoccupied shelters suggests that cavity size is an important attribute of a Hellbender shelter. Median cavity depth was 48% larger for occupied shelters (Table 2) and cavity depth correlated with size of cover rock. Larger cavities likely provide similar benefits to Hellbenders as do larger cover rocks in that they provide greater protection from light and predators. In addition, Hellbenders rock back and forth while resting to enhance oxygen uptake through their skin (Bishop, 1941; Guimond and Hutchinson, 1973). Therefore, Hellbenders may be selecting large cavities to maximize their ability to sway without impediment during periods of low flow when waters may be oxygen-depleted. We did not find any significant relationships between size of cover rock or maximum cavity depth and TL of Hellbenders. Similar findings for size of cover rock and TL of Hellbenders were reported by Hillis and Bellis (1971) and by Humphries and Pauley (2005).

Several variables, including cavity substrate, water depth, and flow rate, did not differ between occupied and unoccupied shelters, suggesting that these variables may not be as important to Hellbenders when selecting a shelter. However, these variables were good indicators of high-quality Hellbender habitat. For example, 93% of occupied shelters and 79% of unoccupied shelters had a cavity substrate of sand and gravel (Fig. 1), with little evidence of silt. Hellbenders probably would not tolerate cavities with large amounts of silt because silt interferes with the Hellbender's already limited ability to take up oxygen (Ultsch and Duke, 1990). In addition, the relatively high flow rates and shallow water depths at both occupied and unoccupied shelters are characteristic of habitats preferred by Hellbenders (e.g., Smith, 1907; Bishop, 1941; Hillis and Bellis, 1971; Humphries and Pauley, 2005).

The results of this study suggest that Hellbenders prefer shelters that maximize the amount of cavity space. Hellbenders selected shelters with cover rocks and cavity depths that were significantly larger than those randomly available in the surrounding habitat. In addition, all the cover rocks of Hellbender shelters had flat bottoms, which also helps define a cavity space. Hellbenders likely prefer larger cavities because they provide greater protection from predators and greater concealment from sunlight. Larger cavities also may allow Hellbenders more space to rock back and forth unimpeded to maximize oxygen uptake through their skin during periods of low flow when oxygen levels drop. Variables such as percent embeddedness, cavity substrate, flow rate, and water depth did not differ between occupied and unoccupied shelters, suggesting that these variables are not as important to Hellbenders when selecting a shelter. However, these variables were indicative of high-quality Hellbender habitat.

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Literature Cited

Alexander, W. P. 1927. The Allegheny Hellbender and its habitat. Buffalo Society of Natural Science 7:13–18.

Bishop, S. C. 1941. The Salamanders of New York. New York State Museum Bulletin 324. University of the State of New York, Albany.

Briggler, J., K. A. Larson, and K. J. Irwin. 2008. Presence of the amphibian chytrid fungus on Hellbenders in the Ozark Highlands. Herpetological Review 39:443–444.

Dundee, H. A., and D. S. Dundee. 1965. Observations on the systematics and ecology of *Cryptobranchus* from the Ozark Plateaus of Missouri and Arkansas. Copeia 1965:369–370.

Foster, R. L., A. M. McMillan, and K. J. Roblee. 2009. Population status of Hellbender Salamanders (*Cryptobranchus alleganiensis*) in the Allegheny River drainage of New York State. Journal of Herpetology 43:579–588.

Gates, J. E., C. H. Hocutt, J. R. Stauffer Jr., and G. J. Taylor. 1985. The distribution and status of *Cryptobranchus alleganiensis* in Maryland. Herpetological Review 16:17–18.

Guimond, R. W., and V. H. Hutchinson. 1973. Aquatic respiration: an unusual strategy in the Hellbender *Cryptobranchus alleganiensis alleganiensis* (Daudin). Science 182:1263–1265.

Hillis, R. E., and E. D. Bellis. 1971. Some aspects of the ecology of the Hellbender, *Cryptobranchus alleganiensis alleganiensis*, in a Pennsylvania stream. Journal of Herpetology 5:121–126.

Humphries, W. J., and T. K. Pauley. 2005. Life history of the Hellbender, *Cryptobranchus alleganiensis*, in a West Virginia stream. American Midland Naturalist 154:135–142.

LeGrand, H. E., Jr., S. P. Hall, S. E. McRae, and J. T. Finnegan. 2010. Natural Heritage Program List of the Rare Animal Species of North Carolina. North Carolina Natural Heritage Program, North Carolina Department of Environment and Natural Resources, Raleigh.

Nickerson, M. A., and J. T. Briggler. 2007. Harvesting as a factor in population decline of a long-lived salamander; the Ozark Hellbender, *Cryptobranchus alleganiensis bishopi* Grobman. Applied Herpetology 4:207–216.

Nickerson, M. A., and C. E. Mays. 1973. The Hellbenders: North American "giant salamanders." Milwaukee Public Museum. 1:1–106.

Nickerson, M. A., and M. D. Tohulka. 1986. The nests and nest site selection by Ozark Hellbenders, *Cryptobranchus alleganiensis bishopi* Grobman. Transactions of the Kansas Academy of Science 89:66–69.

Nickerson, M. A., K. L. Krysko, and R. D. Owen. 2003. Habitat differences affecting age class distributions of the Hellbender Salamander, *Cryptobranchus alleganiensis*. Southeastern Naturalist 2: 619–629.

North Carolina Geologic Survey. 1985. Geologic Map of North Carolina. Department of Natural Resources and Community Development, Division of Land Resources, Raleigh, NC.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC.

Rosgen, D. 1996. Applied River Morphology. Wildland Hydrology Books, Pagosa Springs, CO.

Smith, B. G. 1907. The life history and habits of *Cryptobranchus alleganiensis*. Biological Bulletin 13:5–39.

Ultsch, G. R., and J. T. Duke. 1990. Gas exchange and habitat selection in the aquatic salamanders *Necturus maculosus* and *Cryptobranchus alleganiensis*. Oecologia 83:250–258.

Wheeler, B. A., E. Prosen, A. Mathis, and R. F. Wilkinson. 2003. Population declines of a long-lived salamander: a 20+-year study of Hellbenders, *Cryptobranchus alleganiensis*. Biological Conservation 109:151–156.

Williams, R. D., J. E. Gates, and C. H. Hocutt. 1981. An evaluation of known and potential sampling techniques for Hellbender, *Cryptobranchus alleganiensis*. Journal of Herpetology 15:23–27.

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