Received: 9 June 2020 | Revised: 18 August 2020 | Accepted: 19 August 2020
DOI: 10.1002/rra.3722

RESEARCH ARTICLE

WILEY

Weathering the storm: Improving the availability and stability of artificial shelters for hellbender salamanders

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Funding information
National Science Foundation, Grant/Award Number: IOS-1755055; U.S. Forest Service; U.S. Fish and Wildlife Service

Abstract

Artificial shelters show considerable promise as tools for studying imperiled hellbender salamanders. Their full utility has not yet been fully reached in practice, however, because during initial trials shelters often became blocked by sediment or dislodged during high stream discharge events. To determine whether these challenges could be overcome, we deployed 438 artificial shelters of two different designs across 10 stream reaches and three rivers in the upper Tennessee River Drainage in 2013–2018. We recorded shelter entrance availability during surveys, and recorded which shelters became dislodged following high discharge events. We evaluated two hypotheses: (a) shelter availability was driven by shelter placement and maintenance frequency and (b) shelter stability was driven by shelter design and shelter placement. Shelters were available 78.6% of the time on average (range = 0–100%), and 88.6% (388 of 438) of shelters were stable across all high discharge events. Shelter availability was maximized by clearing sediment from shelter entrances at least once every 40 days (more often in impaired reaches with high siltation) and after large storm events, situating the shelter within 1 m of ≥5 boulders, and orienting shelters such that their entrances do not face directly downstream. Shelter stability with our initial shelter design was 77.5% (169 of 218), but approached 100% (219 of 220) for heavier (40 kg vs. 25 kg) shelters with recessed lids, and in reaches with abundant large boulders. Our findings demonstrate that with an improved design and careful placement, artificial shelters can serve as valuable tools for monitoring hellbenders in reaches with modest siltation.

KEYWORDS
amphibian conservation, aquatic amphibians, artificial habitat, cryptic species, *Cryptobranchus*, monitoring, nest box, survey methods

1 | INTRODUCTION

Although amphibian population declines have been known for several decades (Alford & Richards, 1999; Blaustein et al., 2011; Hopkins, 2007; Houlahan, Findlay, Schmidt, Meyer, & Kuzmin, 2000; Scheele et al., 2019), the secretive life histories of many imperiled species can make identifying the precise causes of their declines difficult (Kellner & Swihart, 2014; Kéry & Schmidt, 2008; Mazerolle et al., 2007), particularly within inaccessible habitats. For example, rocky lotic environments harbor a large number of imperiled amphibian species that use crevices beneath large boulders and other scarcely accessible microhabitats (Kriger & Hero, 2007; Welsh Jr & Ollivier, 1998). Such habitat use makes these species difficult to study, limiting their informed management (Kriger & Hero, 2007; Mensing, Galatowitsch, & Tester, 1998; Olson, Anderson, Frissell, Welsh Jr, & Bradford, 2007; Welsh Jr & Ollivier, 1998). While lifting rocks and debris is sometimes effective for sampling lotic amphibians, doing so often destroys critical microhabitat and is therefore counter to conservation goals (Nickerson, Krysko, & Owen, 2003). Additionally, trapping techniques useful in more lentic aquatic environments, such as hoop nets, crayfish traps, and aquatic drift fences, are often either swept away during high stream discharge events in rocky lotic environments, or require nearly continuous maintenance and monitoring (Browne et al., 2011).

One imperiled species that exemplifies the challenges associated with monitoring lotic amphibians is the hellbender (*Cryptobranchus alleganiensis*). Hellbenders are large, fully aquatic, secretive, long-lived salamanders that tend to thrive in cool, fast-flowing, well-oxygenated streams with moderately deep runs and forested riparian buffers that limit siltation (Beffa, 1976; Briggler et al., 2007; Nickerson & Mays, 1973; Trauth, Wilhide, & Daniel, 1992). Once common across Appalachia and the lower Midwest, hellbenders are declining throughout their range, particularly in reaches experiencing a loss of upstream riparian forest cover (Bodinof Jachowski & Hopkins, 2018). The precise mechanisms underlying hellbender declines are poorly understood, largely because hellbenders are difficult to study, spending the vast majority of their lives hidden under large boulders (Hillis & Bellis, 1971; Humphries, 1999; Keitzer, 2007; Keitzer, Pauley, & Burcher, 2013). Traditional methods for sampling hellbenders have involved manually lifting boulders (Browne et al., 2011), which, although effective, destroys critical hellbender habitat (Nickerson et al., 2003), and is often dangerous for surveyors. Rock lifting surveys are especially harmful between August and April, when male hellbenders are establishing and guarding nests underneath boulders.

Recently, the development of in-situ artificial shelters has presented a less-invasive avenue for studying hellbenders. Artificial shelters for hellbenders are commonly built using the 'boot design' proposed by Briggler and Ackerson (2012), which has subsequently undergone several modifications (Bodinof Jachowski, Briggler, & Hopkins, In Press; Button, 2019; Button, Bodinof Jachowski, Case, Groffen, & Hopkins, In press). Boot design shelters are made from concrete and consist of a rectangular-shaped chamber that hellbenders can access through a single tunnel entrance. Assuming artificial shelters remain consistently secured in place, stay unblocked by sediment, and are used by hellbenders, they have the potential to serve a variety of functions critical for hellbender conservation, including providing eggs for captive rearing, serving as population monitoring tools, improving knowledge about hellbender reproductive biology, and augmenting existing hellbender habitat (Bodinof Jachowski et al., In Press; Bodinof Jachowski, Ross, & Hopkins, 2020).

Despite the potential of artificial shelters, their use thus far has faced several challenges. Past attempts to deploy artificial shelters have often been hindered by shelters becoming either unavailable to hellbenders due to sediment blocking their entrance, or dislodged and damaged during high discharge events (Messerman, 2014). Problems associated with shelter blockage and dislodgement have been so pervasive that some have suggested abandoning boot design shelters entirely (Mohammed, Messerman, Mayhan, & Trauth, 2016). However, one advantage of boot design shelters is that they are less expensive to construct ($30 USD/shelter, not including labor), and easier to transport and deploy than other proposed artificial shelter designs (Bodinof Jachowski et al., In Press). Still, it remains unclear whether challenges associated with using boot design shelters can be ameliorated to an extent sufficient to validate their continued use. Therefore, in this study we sought to determine whether variables related to the construction and deployment of the boot design shelters could influence their availability (i.e., presence or absence of sediment blocking the tunnel) and stability (i.e., ability to withstand high stream discharge events), and thereby improve their utility. We hypothesized that shelter maintenance frequency would drive shelter availability, that shelter design would drive shelter stability, and that shelter placement would drive both. Our study is the first to evaluate ways to maximize the availability and stability of artificial shelters for hellbenders, and thus provides important recommendations for improving their effectiveness.

2 | MATERIALS AND METHODS

2.1 | Artificial shelter construction

From 2013 to 2015, we followed the artificial shelter design specifications of Briggler and Ackerson (2012) and used only as much concrete as was necessary to build shelters, so that they would be easy to carry into streams (Button, 2019). These shelters weighed 25 kg, had 1–2 cm thick walls, and featured raised, custom-fit lids that rested on the dorsal surface of the shelter (Figure 1). Hereafter, we refer to our original shelter design as 'Design A'. After several years of use,

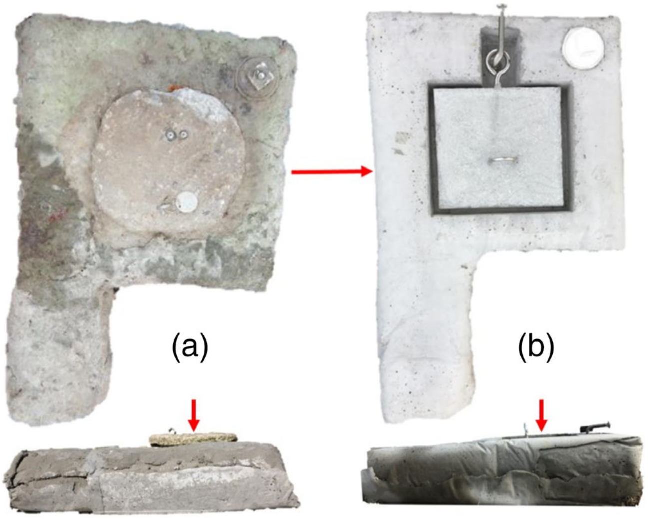

FIGURE 1 Differences in shelter design between Design A (old design; $n = 218$) and Design B (new design; $n = 220$) artificial shelters deployed to sample hellbenders in the upper Tennessee River Basin [Color figure can be viewed at wileyonlinelibrary.com]

numerous Design A shelters were dislodged and damaged due to high discharge events. Therefore, to increase the stability of artificial shelters, in 2016 we modified their design to be heavier (40 kg with 2–4 cm thick walls), and developed a recessed lid design that could be locked in place using an eye-bolt (Figure 1). An important feature of our modified design shelters was that we embedded their lids within a fitted, recessed area with standardized dimensions on the shelter's dorsal surface. Hereafter, we refer to our modified design shelters as 'Design B'.

2.2 | Artificial shelter arrays

Between 2013 and 2018, we deployed artificial shelter arrays at 10 reaches (area = 3,090–5,880 m^2; length = 206–376 channel meters) within three rivers in the upper Tennessee River Basin, in the Ridge-and-Valley and Blue Ridge provinces of southwestern Virginia. To prevent the harassment and illegal collection of hellbenders, we refer to our study rivers as Rivers 1, 2, and 3. We installed shelter arrays within two reaches on River 1, three on River 2, and five on River 3. In total, our study included 438 artificial shelters spread across our 10 study reaches (*n* = 218 for Design A and *n* = 220 for Design B; see Button et al., In press; Button, 2019 for more details). To illustrate potential consequences of sedimentation on shelter availability, we also piloted the use of 30 additional Design B artificial shelters in a silty, heavily impacted reach with low upstream forest cover (57.3%) in the Upper New River Basin.

We installed both Design A and Design B shelters in a wide range of microhabitats potentially suitable for hellbenders at each study reach (Table 1). To minimize spatial autocorrelation in the availability and stability of adjacent shelters, we spaced shelters an average of 10 linear meters apart (range ≈4–30 m). To install shelters, we cleared spaces along the bottom of the stream and embedded shelters within them, deep enough to hold them firmly in place, but shallow enough that shelter tunnel entrances remained unblocked by sediment immediately following installation. We checked artificial shelters every 2–5 days in late summer, and every 2–8 weeks during the rest of the year (Button et al., in review), except during winter and high discharge events when fieldwork was unsafe. We recorded whether shelter entrances were available or were partially to completely blocked by accumulation of sediment (i.e., unavailable) on each survey, and immediately cleared all blocked tunnels. Following high discharge events, we recorded which shelters became dislodged.

2.3 | Data collection

We predicted that multiple variables related to in-stream conditions and survey frequency would impact shelter availability or stability. Therefore, we assessed the influence of average days in between

TABLE 1 Mean values and ranges for all variables used in our shelter availability and stability analyses

Variable	Mean, or probability of presence	Range	Variable type	Analyses used in	Assessment of metric
Channel transition status	0.47	0 or 1	Binary	Availability	Visual
Pool-riffle-run transition status	0.15	0 or 1	Binary	Availability	Visual
Sand/gravel bar transition status	0.36	0 or 1	Binary	Availability	Visual
Average days between shelter maintenance	36.93	3.00–112.00	Continuous	Availability	Computed
Distance to bank (m)	3.70	0.10–9.30	Continuous	Availability	Tape measure
Tunnel angle ( )	24.65	0.00–105.00	Continuous	Availability	See Button (2019)
Upstream CWR forest cover (%)	62.6	53.6–70.4	Continuous	Availability	See Button (2019)
Water depth at tunnel (cm)	44.21	19.00–103.00	Continuous	Availability	Meter stick
Current velocity parallel to current (m/s)	0.28	−0.13 to 10	Continuous	Availability	See Section 2
Current velocity perpendicular to current (m/s)	0.13	0.00–0.66	Continuous	Availability	See Button (2019)
Anchor rock presence	0.22	0 or 1	Binary	Stability	Visual
Design	Design A: *n* = 218 Design B: *n* = 220	NA	Category	Stability	NA
High discharge events experienced	7.37	0–24	Count	Stability	See Section 2
Boulders within 1 m	5.42	0–11	Count	Both	Visual
Reach-wide large boulder density (count from reach-wide survey)	36.98	14–85	Count	Both	See Button (2019)

Note: Variables of binary (present/absent) character are coded as 0 or 1, therefore their mean values represent the percentage of shelters where we considered them present. For our assessments of metrics, 'visual' = not requiring any specialized tool to measure; 'computed' = not directly measured during fieldwork but calculated thereafter; 'tape measure' = measured linear distance using a tape measure; 'see methods' = described previously in Section 2.3.

surveys, angle formed between the direction of the tunnel and direction of the current ('tunnel angle' hereafter — where tunnel angle = 0 if the tunnel faces directly downstream and 90 if it faces directly toward the bank), current velocity at the tunnel parallel and perpendicular to the current, presence or absence of a pool-riffle-run transition, steeply cut channel (>10% incline on both sides), and sand/gravel bar (a patch of >1 m^2 with >50% sand/gravel) within 5 m of the shelter, and percent forest cover in the upstream catchment-wide riparian (CWR) area (Bodinof Jachowski & Hopkins, 2018) on shelter availability (Table 1; see Button et al., In press; Button, 2019 for more details). To ensure that our measurements accurately reflected typical stream conditions, we measured all variables that changed with flow conditions (current velocity at each shelter, shelter depth, and shelter distance from bank) when stream discharges were at their approximate annual medians (Table 2; Button et al., In press). We also assessed the influence of number of high discharge events experienced, shelter design, and whether or not a shelter was braced by at least one anchor rock (i.e., at least one large, embedded boulder placed firmly against the shelter to keep it in place during high discharge events) on shelter stability. We quantified the number of high discharge events experienced by each shelter using data from the nearest USGS gage within each respective stream (Table 2). If the daily discharge at the nearest USGS stream gage was >×4 the annual mean discharge for at least one full day (as typically required for a shelter to become dislodged), we considered the stream to have experienced a 'high discharge' event that day.

2.4 | Data processing and analyses

We used average shelter availability (i.e., times available [n = 0–72] divided by times surveyed [n = 1–76]) and shelter stability (i.e., stable or dislodged) as response variables in all analyses, and used a multistep procedure to model our results. After verifying that $|r| < 0.6$ for all possible pairs of predictor variables (Supporting Information Tables S1 and S2), we used PERMANOVA and betadisper analyses to determine whether our predictor variables were collectively related to shelter availability and stability (Dixon, 2003), and used nonmetric multidimensional scaling (NMDS) plots (Kruskal, 1964) to visualize the results (Supporting Information Figures S1 and S2). PERMANOVA analyses determine whether the average ordinated coordinates of datapoints containing multiple predictor variables are related to a chosen response variable (i.e., shelter availability or stability; analyzed separately), while betadisper analysis determines whether the dispersion of these ordinated coordinates is related to the response variable.

After validating our chosen sets of predictor variables using PERMANOVA and betadisper analyses, we used boosted regression trees (BRTs; Elith, Leathwick, & Hastie, 2008) to assess associations between individual predictor variables (Table 1) and shelter availability and stability, using the 'gbm' package in R (Version 3.3.3, R Core Development Team). We treated shelter stability as binomially distributed and average shelter availability as beta-distributed in all BRT analyses. Boosted regression trees were a desirable modeling approach given our study questions, because they tend to be useful for identifying ecological thresholds due to their use of split points (Elith et al., 2008), and perform better than other approaches for datasets that contain spatial structure (Crase, Liedloff, & Wintle, 2012).

We modeled shelter availability and stability using two separate BRTs, built initially using all applicable predictor variables, then rebuilt after discarding variables of minimal importance (i.e., <5% relative influence on the model). Additionally, we discarded variables from our refined models if their inclusion in the model weakened its performance. We used cross-validated correlation scores and standard errors to evaluate the performance of our availability BRTs (Elith et al., 2008), and used cross validated AUC scores and standard errors built using k-fold cross validation (Kohavi, 1995) to evaluate the performance of our stability BRTs. We built shelter availability models using tree complexity = 2, learning rate = 0.0005, and bag fraction = 0.5 (De'Ath, 2007), because initial model runs suggested these settings optimized model performance. For shelter stability, we built models using tree complexity = 2, learning rate = 0.01, and bag fraction = 0.75.

TABLE 2 Median, minimum, and maximum daily discharges (in m^3/s) over the period of shelter deployment for each river containing artificial shelter arrays, and ranges of distances to the nearest USGS gage for study reaches in each river

River	Period of shelter deployment	Median	Minimum	Maximum	Channel kilometer between USGS gage and study reaches (range)
River 1	June 2018 to Present	2.95	1.64	11.78	23.28–40.77
River 2	June 2014 to Present	3.26	0.85	1,220	15.33–22.75
River 3	May 2013 to Present	2.38	0.65	51.54	0.05–17.72

Note: We calculated predictor variables that varied with stream discharge when the discharge of each river was at its approximate annual median. High maximum daily discharges (relative to the median) over the course of the study illustrate the flashy, flood-prone nature of our study rivers. On River 1, two study reaches were located 8.72–12.34 channel km upstream of the nearest USGS gage, and three were located 0.05–17.72 km downstream of the gage. All River 2 and River 3 study reaches were located upstream of the nearest USGS gage.

To account for the relationship between the number of surveys of a shelter and the expected accuracy of its estimated availability, we weighted shelters in our availability BRTs using a logarithmic scale, based on number of times surveyed (Supporting Information Figure S3; see also Button et al., In press). This allowed us to filter our 6,793 total shelter surveys down to a single average value for each shelter (n = 438) while accounting for the relative amount of uncertainty in our estimate of average shelter availability at these shelters.

We evaluated the influence of individual variables based on their relative influence in our refined models, and visualized this influence using partial dependence plots. To determine whether any pairs of predictor variables had an interactive relationship with shelter availability or stability, we used the procedure described by Elith et al. (2008).

3 | RESULTS

Artificial shelters were available 78.6% of the time (individual shelter range = 0–100%), and 388 of 438 shelters (88.6%) were stable during all high discharge events experienced. The two rivers with multiyear arrays (Rivers 2 and 3) experienced respective totals of 24 and 21 high discharge events over the course of the study, while River 1 experienced only a single high discharge event after installing shelters there in May–July of 2018. Design A shelters were more likely to lose their lids than Design B (34.4% [75 of 218] vs. 0% [0 of 220]), and also became dislodged much more frequently than Design B shelters (22.5 vs. 0.5%). Differences in the stability of Design A and Design B increased with time since deployment (Figure 2), and 80% (40 of 50) of unstable shelters were dislodged within the first 11 high stream discharge events experienced following their deployment.

In our pilot study of Design B artificial shelter availability at a silty, heavily impacted reach within the Upper New River Basin, 90 % of shelter entrances became blocked by sediment within a week of shelter maintenance under base flow conditions. However, none of these shelters ever lost their lids or became dislodged.

Our multivariate analyses strongly suggested that shelter characteristics were related to average shelter availability (F = 5.29 and p = .001 for betadisper; F = 4.66 and p = .001 for PERMANOVA) and stability (F = 59.33 and p < .001 for betadisper; F = 6.28 and p < .001 for PERMANOVA). Betadisper analyses provided particularly strong evidence that the dispersion of our ordinated predictor variables was related to shelter availability (r = 0.31 between average shelter availability and distance to median centroid among our ordinated predictor variables) and stability (average distance to centroid = 3.35 NMDS units for stable shelters versus 2.00 for dislodged shelters). However, given the significance our betadisper analyses, our PERMANOVA results should not be viewed as universally applicable to other hellbender datasets (Dixon, 2003). The influence of shelter availability and stability on datapoint dispersion suggested that our two sets of predictor variables were collectively informative of their respective response variables, and therefore appropriate to use in future BRT models.

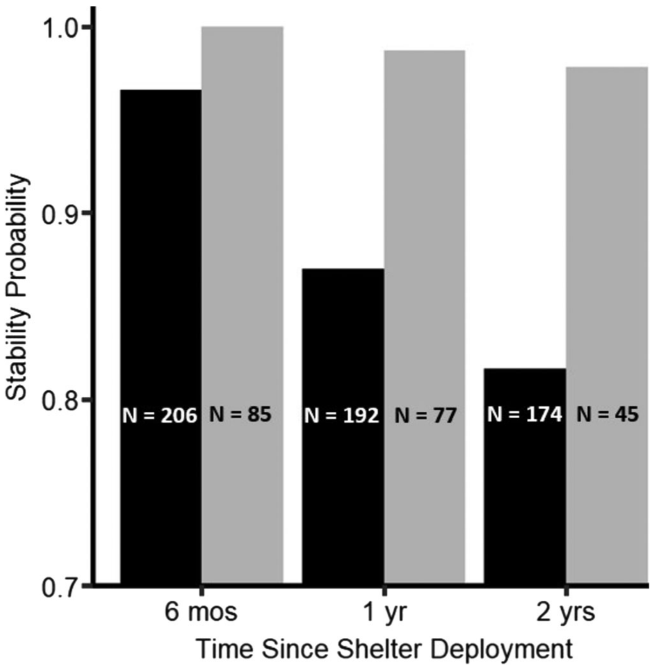

FIGURE 2 Shelter stability for Design A (black) and Design B (gray) hellbender artificial shelters deployed in the upper Tennessee River Basin, 6 months, 1 year, and 2 years after deployment

3.1 | Factors influencing shelter availability

After removing unimportant variables, we retained shelter maintenance frequency, number of boulders within 1 m (Wolman, 1954), percent upstream CWR forest cover, and tunnel angle as informative predictors in our final shelter availability BRTs (Figure 3). Shelter availability increased with number of boulders within 1 m, upstream CWR forest cover, and tunnel direction relative to the direction of stream current (i.e., tunnel angle; up to at least 65), and was inversely related to average number of days between shelter maintenance. Days between shelter maintenance, number of boulders within 1 m, and upstream CWR forest cover contributed the most to the model, and had respective relative influences of 33.0, 29.2, and 24.1%. We found no evidence of pairwise interactions among our predictor variables. Our cross-validated model predictions were 40% correlated with actual average availability values at artificial shelters (SE = 4% among model runs).

3.2 | Factors influencing shelter stability

We retained density of reach-wide boulders >40 cm long, number of high discharge events experienced, number of boulders within 1 m, and shelter design as informative predictors in our final BRTs for shelter stability (Figure 4). Shelter stability was highest when shelters were built using Design B and deployed in reaches with high densities of large boulders (i.e., > 68.5 large boulders encountered on 10 equally spaced transects across the reach), and dislodged shelters were

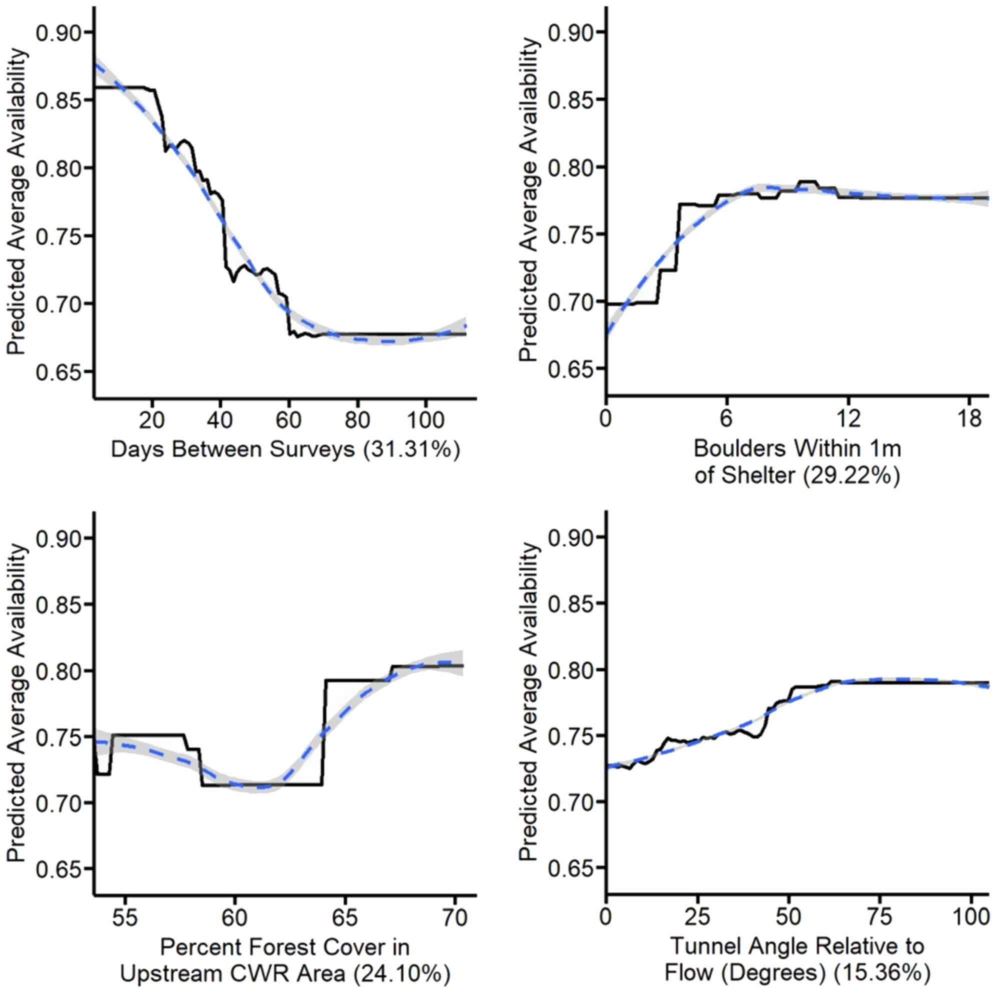

FIGURE 3 Partial dependence plots with shelter availability predictions for important predictor variables retained in the final version of our shelter availability model. Percentages shown on the *x*-axis represent relative variable influence. Solid black lines show fitted functions, while shaded areas represent 95% percentile-based confidence intervals built using 200 bootstraps [Color figure can be viewed at wileyonlinelibrary.com]

usually lost within the first 11 high discharge events they experienced. Shelter stability was also related to the number of boulders within 1 m, but the effect of this predictor was relatively small (10.1% variable influence) and inconsistent (Figure 4). In total, 77.5% of Design A shelters and 99.6% of Design B shelters were stable across all high discharge events experienced. Number of high discharge events experienced (49.2% variable influence) and shelter design (24.3% variable influence) were the most important variables in the stability BRT model (Figure 4). Although instream variables substantially influenced shelter stability for Design A, there were strong interactions between shelter design and our other predictor variables, and the predicted stability of Design B never dropped below 97.0% (Figure 4). Model predictions of shelter stability were exceptionally accurate (cross-validated AUC = 0.91, *SE* = 0.02).

4 | DISCUSSION

We sought to determine how artificial shelters should be built and deployed to maximize their availability to hellbenders and stability through high stream discharge events. The sensitivity of shelter availability to maintenance frequency, number of boulders within 1 m, percent upstream CWR forest cover, and tunnel angle relative to stream flow suggests that shelters can be made available to hellbenders under circumstances of modest stream impairment if deployed optimally and maintained with sufficient frequency. Further, the superior stability of our Design B shelters demonstrates that the efficacy of boot design shelters can be greatly enhanced with simple modifications to construction. In light of the problems encountered during the initial years of artificial shelter use for hellbenders (Bodinof Jachowski, Millspaugh, & Hopkins, 2016; Messerman, 2014), our solutions to these problems are encouraging.

Artificial shelters have the potential to improve hellbender monitoring capabilities only if their entrances remain unblocked by sediment. Shelter maintenance frequency was an important driver of shelter availability, and the relationships revealed by our availability BRTs (Figure 3) suggested that maintaining shelters every 40 days was usually sufficient to keep their entrances unblocked >75% of the time. This is less often than the maintenance frequency required for certain other traps and enclosures that are commonly used in streams (Beachy, 1997; Jung, Droege, Sauer, & Landy, 2000; Pauley & Little, 1998), and may also be an overestimate of shelter maintenance needs during periods of low or average discharge, when shelters become blocked relatively infrequently compared to during high

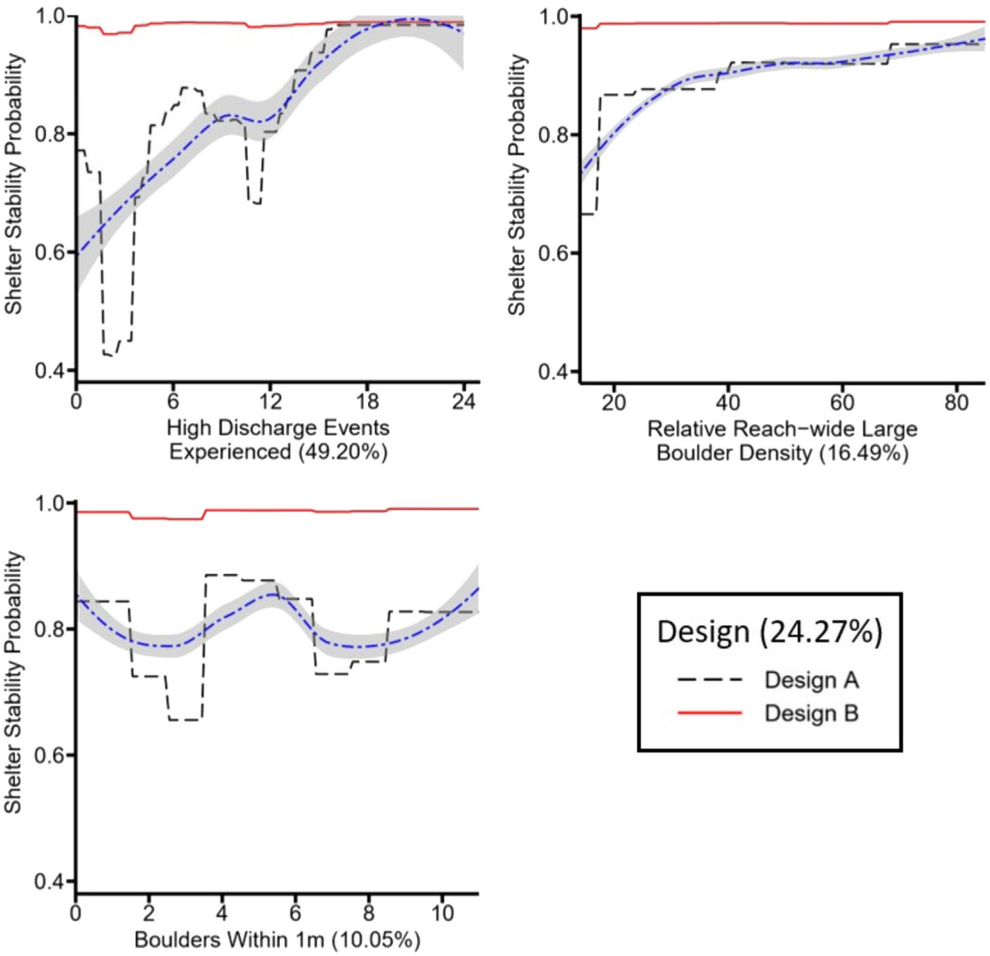

FIGURE 4 Plots of the interactive relationships of shelter design and all other relevant predictor variables with shelter stability. Percentages shown on the *x*-axis represent relative variable influence. Solid lines show fitted functions, while shaded areas represent 95% percentile-based confidence intervals built using 200 bootstraps [Color figure can be viewed at wileyonlinelibrary.com]

discharge events. Additionally, while most groups using artificial shelters have sought to limit within-shelter sedimentation by orienting shelter tunnels directly downstream, our finding that shelter availability increased with tunnel angle relative to current direction (up to at least 65°) suggests that slightly pivoting the tunnel entrance from the direct downstream direction may best minimize sediment-depositing microcurrents around the tunnel entrance. Importantly, pivoting shelter entrances to not face directly downstream does not appear to reduce shelter occupancy by hellbenders (Button et al., In press).

Because siltation is the principal cause of shelter blockages, the utility of artificial shelters may be limited in heavily impacted systems where the loss of riparian buffers or other disturbances has increased sediment loading in the stream. Our finding that shelter availability decreased sharply with loss of upstream forest cover is a likely consequence of riparian buffer removal, and is unfortunate given that riparian deforestation, and subsequent siltation, are often highest in watersheds where hellbenders are most at risk of extirpation (Bothner & Gottlieb, 1991; Wheeler, Prosen, Mathis, & Wilkinson, 2003; Williams, Gates, Hocutt, & Taylor, 1981). Thus, a conflict exists between the need for effective hellbender monitoring tools and the practicality of using artificial shelters to fulfill this need in heavily impacted streams. This limitation is further illustrated by our finding that 90 % of shelter entrances at our silty, heavily impacted pilot reach in the Upper New Basin became blocked by sediment within a week of shelter maintenance under base flow conditions; far more rapidly than at any of our upper Tennessee River Drainage arrays. It remains unclear whether other site characteristics such as stream order and gradient influence sediment deposition in shelter tunnels. Thus, it may be useful to pilot the use of a few shelters at impaired stream reaches of interest prior to investing resources toward deploying entire arrays of shelters in such reaches.

While the availability of artificial shelters was constrained by environmental conditions such as sediment loading, we found that shelter stability was achievable >99% of the time by using our modified shelter design (Design B) and following standard shelter installation procedures, such as embedding shelters in the streambed and anchoring them firmly in place. The near-perfect stability of Design B shelters is impressive given that they endured several severe flood events, including multiple tropical depressions and heavy spring thunderstorms that increased stream discharges at nearby USGS gages (Table 3) up to ×20 their mean level (United States Geological Survey, 2020), and displaced large boulders and substantially altered channel geomorphology in some places (pers. obs.). Despite the strength of flood events during our study, only 0.5% (1 of 220) of Design B shelters ever became dislodged, in contrast with the 22.5% (49 of 218) dislodgement observed for Design A (Figure 2). The

TABLE 3 Recommendations for artificial shelter placement and post hoc decision making, given the explicit objective of maximizing shelter availability and stability

Variable		
Availability	**Recommendation**	**Importance**
Maintenance frequency	Check artificial shelters and clear blocked tunnels as often as feasible, but at least every 40 days.	Very high
Adjacent boulders	Situate shelters within 1 m of at least five large boulders.	Very high
Habitat quality	Pilot the use of a few shelters in impaired reaches with low upstream CWR forest cover and high sediment loads before committing resources to deploying entire arrays at these reaches. Maintain shelters in impaired reaches more frequently than elsewhere.	Moderate–high
Tunnel angle	Orient shelters such that tunnel angle is 45–65 + (slightly pivoted away from directly downstream).	Moderate
Stability		
Shelter design	Build shelters with thick walls and recessed lids anchored by an eye-bolt and hook (Design B).	Very high
High discharge events experienced	Do not move productive (i.e., used, available, and undamaged) shelters that have survived >11 high discharge events.	Very high
Reach-wide large Boulder density	If design A shelters are the only shelters available, they may be most stable in reaches with high densities of boulders which likely serve as roughness elements in the stream substrate.	High

Note: We defined the importance of each recommendation qualitatively, based on a combination of the relative influence of each variable in our availability or stability BRTs and the effect size of each variable's influence.

superiority of Design B is also evident in the fact that their predicted stability never dropped below 97% in our analyses, regardless of the values of all other predictor variables (Figure 4).

We attribute observed differences in the stability of our two shelter designs to the superior structural integrity and recessed lids of Design B. Specifically, Design B shelters have 1–2 cm thicker walls and are 15 kg heavier than those built using Design A, and have multiple apparent advantages in their lid design. Design B lids have the advantage of being made from a mold, making it possible to replace dislodged lids quickly in the field without having to remove the shelter from the stream to build a new custom-fitting lid. Remarkably, however, we never had to replace the lid of a Design B shelter, despite needing to do so at 34.4% of shelters built using Design A. We believe this occurred because the recessed nature of Design B lids caused them to experience less drag force than Design A, which likely reduced the amount of force exerted onto them by the current (Dey, 2014). Additionally, Design B lids are anchored in place using an eye-bolt and hook, and often become locked in place when the seam between the lid and shelter fills with sand particles, sometimes requiring a sturdy tool (e.g., screwdriver) to pry open. Design A shelters, by contrast, are held in place with stainless steel brackets that tend to rust and eventually break, and lack the exposed seam between the lid and shelter necessary for accumulating sand particles to lock the lid in place. The superiority of Design B lids has important ramifications for shelter stability, because shelters prone to losing their lids were the ones that became dislodged most often during high discharge events (pers. obs.), suggesting that lid loss increases the odds of shelter dislodgement. Thus, the instability of Design A shelters would likely have been even worse in our study had we not acted to minimize shelter dislodgement immediately following high discharge events by locating and re-attaching lids that had been swept off of Design A shelters.

Although we did not set out to evaluate the structural integrity of the artificial shelters after prolonged deployment in the field, our anecdotal observations suggest that Design B shelters will also be longer-lived than Design A shelters. Even when stable, Design A shelters often developed exposed metal within 5 years of deployment, and had to be removed due to safety concerns for occupying animals. While we deployed Design B shelters more recently, within the past 3 years, we do not expect them to deteriorate as quickly as Design A given their thicker walls, because concrete thickness and deterioration rates of instream structures are inversely related (Zhao & Chen, 2001).

The improved stability of Design B shelters relative to Design A comes with a couple minor practical drawbacks. For example, Design B shelters cost $8 more to construct than Design A, due to the additional amount of concrete needed. In addition, Design B shelters are more difficult for a single person to carry into streams and deploy than Design A as a result of their heavier weight (40 kg vs. 25 kg). However, Design B shelters can be efficiently transported by two people using a sturdy stretcher (i.e., platform with four handles) on land and an inner tube with a canvas cover within the stream. Taken together, we found that the superior performance of the new shelter design outweighs these practical considerations.

Because Design A shelters are already deployed in many watersheds across the hellbender's geographic range, our findings point to multiple factors that will improve their utility. Our results suggest that the instability of Design A shelters can be partly mitigated by keeping productive (i.e., used, available, and undamaged) shelters that have survived numerous high discharge events in place (Figure 4), since

80% of shelters destined for dislodgement were lost prior to a threshold of number of high discharge events in our study (>11). In addition, our results suggest that shelter stability improves considerably when shelters are placed in reaches with high densities of large boulders (i.e., >68.5 large boulders encountered during 10 equally spaced transects across the reach [16.5% relative influence]), possibly because boulders serve as roughness elements in stream substrate that reduce average current velocity (Ferguson, 2007), which should thereby reduce the amount of force exerted against artificial shelters. We have anecdotally observed decreased shelter stability in reaches that lack these roughness elements and consist mostly of bedrock. Interestingly, water depth and current velocity at median stream discharge were not informative predictors of shelter stability, indicating that shelter design, proper installation, and stream substrate characteristics are the primary considerations for enhancing shelter stability.

Our study demonstrates that the struggles caused by shelter dislodgement in prior studies (Bodinof Jachowski et al., 2016; Messerman, 2014) are potentially mitigated by simple adjustments to artificial shelter design and installation. Ongoing efforts to develop entirely new artificial shelter designs, such as the hydrodynamic shelters (Mohammed et al., 2016), will hopefully yield similar promising results. Additional research is needed to determine whether additional design elements can reduce sediment blockage of tunnels, though we suspect that factors related to reach-level sedimentation and microhabitat features at the tunnel entrance will influence tunnel availability regardless of shelter design. Although our modified Design B shelters are occupied as frequently by hellbenders as the original Design A shelters (Button et al., In press), features of different artificial shelter designs that influence their attractiveness to hellbenders also require future assessment.

ACKNOWLEDGMENTS

We thank J. D. Kleopfer for his invaluable support throughout the study, multiple generous landowners who allowed us to access streams through their properties, and Drs. Bryan Brown and Joel Snodgrass for their helpful feedback on this manuscript. We would also like to thank Henry Davie, John Connock, Clara Frazier, Matt Lacey, Tiffanie Pirault, Alex Grimaudo, Valentina Alaasam, Jeronimo Gomes Da Silva Neto, Hank Vogel, Georgia Martin, and Silas Beers for their assistance in the field and help constructing and installing artificial shelters. This research was supported by the Virginia Department of Game and Inland Fisheries and partially funded through a State Wildlife Grant from the U.S. Fish and Wildlife Service. Additional funding was provided by the U.S. Forest Service and a National Science Foundation grant (IOS-1755055) awarded to W.A.H. All protocols were approved under the Virginia Department of Game and Inland Fisheries handling permit (Virginia DGIF Permit No. 060465) and the Virginia Tech Institutional Animal Care and Use Committee (VT IACUC Numbers 16-162, 13-128, 11-140, and 08-085).

CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Button ST, Hallagan JJ, Bodinof Jachowski CM, Case BF, Groffen J, Hopkins WA. Weathering the storm: Improving the availability and stability of artificial shelters for hellbender salamanders. *River Res Applic*. 2020;36: 1944–1953. https://doi.org/10.1002/rra.3722