variables through visual estimation, and defined pools, riffles, and runs using the same criteria as Dey (2014). We used a tape measure to determine whether a variable was present within 5 m of a shelter.

Microhabitat scale.—Given that microhabitat features are often important drivers of resource use in nonvagile species (Welsh and Ollivier 1998), we assessed the influence of several microhabitat-scale variables (i.e., at or within 1 m of the shelter) on both occupancy and nesting. We measured the angle formed between the direction of each shelter's tunnel and the direction of stream current (''tunnel angle''); current velocity at the tunnel parallel to, and perpendicular with, the current (''downstream current velocity'' and ''bank-to-bank current velocity,'' respectively [m/s]); water depth at the tunnel entrance (cm); shelter distance to the bank (m); percentage of canopy cover above the shelter; vertical distance to canopy (m, where applicable); and the number of crevice-bearing boulders within 1 m of the shelter. To determine tunnel angle, we attached a fishing bobber to the end of a 50-cm-long string, held the opposing end of the string at the water's surface above the base of the tunnel, and measured the angle formed between the string and the tunnel using a protractor. We used a 2D FlowTracker2 Handheld-ADV flow meter (Xylem Inc.) placed at $6/10^{\text{ths}}$ the depth of the stream to assess downstream and bank-to-bank current velocity, and measured water depth at the tunnel entrance with a meter stick. Using a tape measure, we calculated distance to bank, then combined this measurement where applicable with a clinometer-based angle to above-shelter canopy taken from the bank to determine vertical distance to canopy. To estimate percentage of canopy cover, we photographed the canopy above each shelter using a fisheye lens (GoPro Inc.), digitally overlaid a densiometer-style grid of 96 dots onto each photo, and multiplied the number of dots that intersected canopy by 1.04 (Lemmon 1956). We considered boulders (b-axis 2: 256 mm; Wolman 1954) within 1 m of shelters to be crevice-bearing using the same criteria used for determining reach-scale boulders. We measured all discharge-dependent variables once, when discharge at the nearest US Geological Survey stream gauge (Table 1; USGS 2019) was at its approximate annual median.

Time since installation and density of Hellbenders.—In addition to being influenced by multiscale habitat variables, we predicted that shelter occupancy and nesting would increase over several years following shelter installation, and increase concomitant with adult/subadult density of Hellbenders. We used average months since shelter installation across all surveys to model shelter occupancy, and used number of breeding seasons since shelter installation to model shelter nesting. To evaluate the influence of density of Hellbenders on shelter use, we used existing density estimates from five of our six multiyear reaches (Hopkins and Jachowski 2018), and estimated density at the sixth using a single-season Huggins closed-capture model (Huggins 1989) in 2018 (Appendix S-I, Supplemental Material). In this instance, we considered detection across our two surveys of the reach constant given the short timespan between these surveys, and variable between individuals. Reach-scale densities of large boulders bearing suitable crevices explained 80% of the variation in densities of Hellbenders across our study reaches (W.A. Hopkins, personal observation).

Shelter design.—Button et al. (2020) reported that artificial shelters should be constructed with thick walls, heavy frames, and inset lids to improve stability during high stream discharge events. Therefore, we assessed whether Hellbenders occupied and nested in shelters built using a heavy, sturdy design (*n* ¼ 220) as often as shelters constructed using the original, more lightweight design (*n* ¼ 218; Briggler and Ackerson 2012). In doing so, we sought to verify that no tradeoff existed between shelter stability and shelter use.

Data Processing and Analyses

Response units.—We used average occupancy and nesting at individual artificial shelters as our response variables in all analyses. To estimate average occupancy by Hellbenders at each artificial shelter, we divided the number of surveys in which we found each shelter occupied (*n* ¼ 0–64) by our total number of surveys of the shelter (*n* ¼ 1–76). To calculate average shelter nesting, we divided the number of breeding seasons in which Hellbenders nested in each shelter (*n* ¼ 0–4) by the total number of breeding seasons that each shelter was in place (*n* ¼ 1–6).

Combining habitat and density.—We predicted that occupancy and nesting in artificial shelters would be greatest in reaches that contained limited natural habitat for Hellbenders relative to their densities of adults/subadults (Jachowski et al. 2020). To scale the suitable habitat relative to densities of adult/subadult Hellbenders, we developed a standardized habitat surplus metric by subtracting estimated densities of adult/subadult Hellbenders from large suitable boulder density estimates within each study reach. The surplus values were scaled such that values ranged between 0 and 1.

Two-step analytical approach.—To assess relationships between predictor variables and shelter use by Hellbenders, we adopted a two-step analytical approach from Button et al. (2020). Specifically, we first used permutational multivariate analysis of variance (PERMANOVA) and betadisper analyses to determine whether our predictor variables had a significant collective influence on shelter use. Then, we used boosted regression trees (BRTs) to identify precise relationships between individual predictor variables and shelter use.

Multivariate analyses.—We verified that our set of predictor variables influenced shelter use by Hellbenders using PERMANOVA and betadisper analyses, which determine whether the location and dispersion of points from an ordinated set of predictor variables are related to values of a chosen response variable (i.e., average shelter occupancy/nesting; Dixon 2003). Significant results obtained from PERMANOVA and betadisper analyses provided assurance that any trends reflected actual associations between predictor and response variables (rather than misinterpretations of random differences in the occupancy and nesting use of shelters). Neither PERMANOVA nor betadisper are robust to missing values (Oksanen et al. 2008). Therefore, prior to conducting all multivariate analyses, we used random forest imputations (Stekhoven and Bühlmann 2011) to generate values for missing data (~10% of data used from both datasets, because of limitations imposed on

TABLE 3.—Scores of models predicting occupancy and nesting activity by Hellbenders (*Cryptobranchus alleganiensis*) in artificial shelters deployed within the Upper Tennessee River drainage. Model A ¼ habitat variables from all three spatial scales used during initial model construction; Model B ¼ built with reach-scale predictors excluded during initial model construction; Model C ¼ reach- and core habitat–scale variables excluded during initial model construction; Model D ¼ time since shelter installation and the reach-scale density of Hellbenders as the only predictor variables; Model E ¼ same predictor variables as the top model, but built using data from our six original study locations only. The top performing models are indicated in boldface.

Model	Cross-validated correlation	Cross-validated SE
Occupancy		
A	0.658	0.043
B	0.655	0.024
C	0.655	0.024
D	0.651	0.049
E	0.649	0.039
Nesting		
A	0.278	0.042
B	0.205	0.062
C	0.205	0.062
D	0.256	0.047
E	0.215	0.056

data collection by high stream discharges during 2018). We excluded data from reaches sampled for only a single year (hereinafter, ''single-year reaches'') from both sets of PERMANOVA and betadisper analyses because their inclusion would have required imputing -20% of values for both datasets, given that single-year reaches lacked population density estimates. We standardized all nonbinary predictor variables so that their minimum and maximum values equaled 0 and 1, respectively, and constructed distance matrices for both datasets using Euclidean distances (Lele and Richtsmeier 1991). We performed all multivariate analyses using the vegan package in R (v3.3.3; R Core Development Team 2017).

To visualize the relationships identified by PERMANOVA and betadisper analyses, we generated nonmetric multidimensional scaling (NMDS) plots (Appendix S-II, Supplemental Material). This approach uses distance matrices to collapse data points containing several variables into a specified number of dimensions (Kruskal 1964). We carried out NMDS ordinations for average shelter occupancy and nesting using the minimum number of dimensions where stress was ‚0.2 (Anderson 2001).

Boosted regression trees.—After verifying that our predictor variables were informative of shelter use via PERMANOVA and betadisper analyses, our second step was to use BRTs to determine the influence of individual predictor variables on occupancy and nesting, using the gbm package in R (v3.3.3; R Core Development Team 2017). BRTs use iterative decision trees to model the influence of predictor variables on a chosen response, and weight each tree based on how much its inclusion in the model minimizes the loss function (Elith et al. 2008). The influence and importance of individual predictor variables is subsequently determined based on their prevalence and average influence across the weighted set of decision trees. Boosted regression trees tend to be useful for identifying ecological thresholds (Elith et al. 2008), and often outperform other modeling approaches (e.g., generalized linear models and generalized additive models) for datasets that are spatially autocorrelated (Crase et al. 2012). We modelled shelter occupancy and nesting activity using separate sets of BRTs, and used average shelter occupancy across all surveys, or average nesting across all breeding seasons, as our unit of replication. Because both response variables had continuous distributions between 0 and 1, we treated them as beta-distributed in all BRT analyses. To account for the differing uncertainty associated with average occupancy and nesting estimates calculated for shelters surveyed or available for nesting differing numbers of times, we assigned shelters weights in our models based on the number of times we surveyed them, or number of breeding seasons they experienced. Specifically, we adopted the approach from Button et al. (2020) to develop a weighting scale that incorporated average occupancy and nesting at shelters, rather than shelter occupancy and nesting during individual shelter surveys, as our unit of replication (Appendix S-III, Supplemental Material).

We included data from all study reaches in our BRTs, including single-year reaches that lacked estimates of population densities of Hellbenders (two on River 1, and two on River 2). Shelter use and habitat data from single-year reaches were valuable even in the absence of density estimates, because we collected these data 5–90 d after shelter installation (*n*¼318 occupancy and 59 nesting data points), and when differences in shelter occupancy among reaches increased most rapidly (Jachowski et al. 2020). Whereas the inclusion of single-year study reaches in our models did not substantially alter our results, the superior performance of these models corroborated the utility of including single-year reaches in our models (Table 3). This is expected given that BRTs exclude missing values when fitting tree nodes, thus preventing missing data from substantially influencing the shape and slope of modeled relationships. We excluded data from both study reaches in River 1 from our nesting BRT, however, because we were unable to survey these reaches for nests on account of continuously high stream discharge during the 2018 breeding season.

We evaluated BRT performance based on the correlation of model predictions with observed occupancy and nesting values (i.e., cross-validated correlation) using k-fold cross-validation with five folds (Kohavi 1995). We compared models based on their cross-validated predictive performance (Elith et al. 2008). After constructing initial models, we removed variables with ‚5% contributions, ran these models again, and repeated this process until all variables contributed at least 5% to the model, to avoid overfitting. We also dropped additional variables from our refined models if their inclusion in the model worsened its performance. Based on the cross-validated correlation between predicted and actual response data, we built all models using tree complexity ¼ 2, learning rate ¼ 0.0005, and bag fraction ¼ 0.5, because these values maximized model performance during preliminary model building (Elith et al. 2008). We evaluated the influence of individual predictor variables on shelter occupancy and nesting activity using partial dependence plots (which make predictions by varying a single predictor variable while holding the others constant at their mean) and relative variable influence for predictor variables retained in our top-performing models.

To determine whether including reach-scale variables in our models reduced the estimated influence of finer-scale

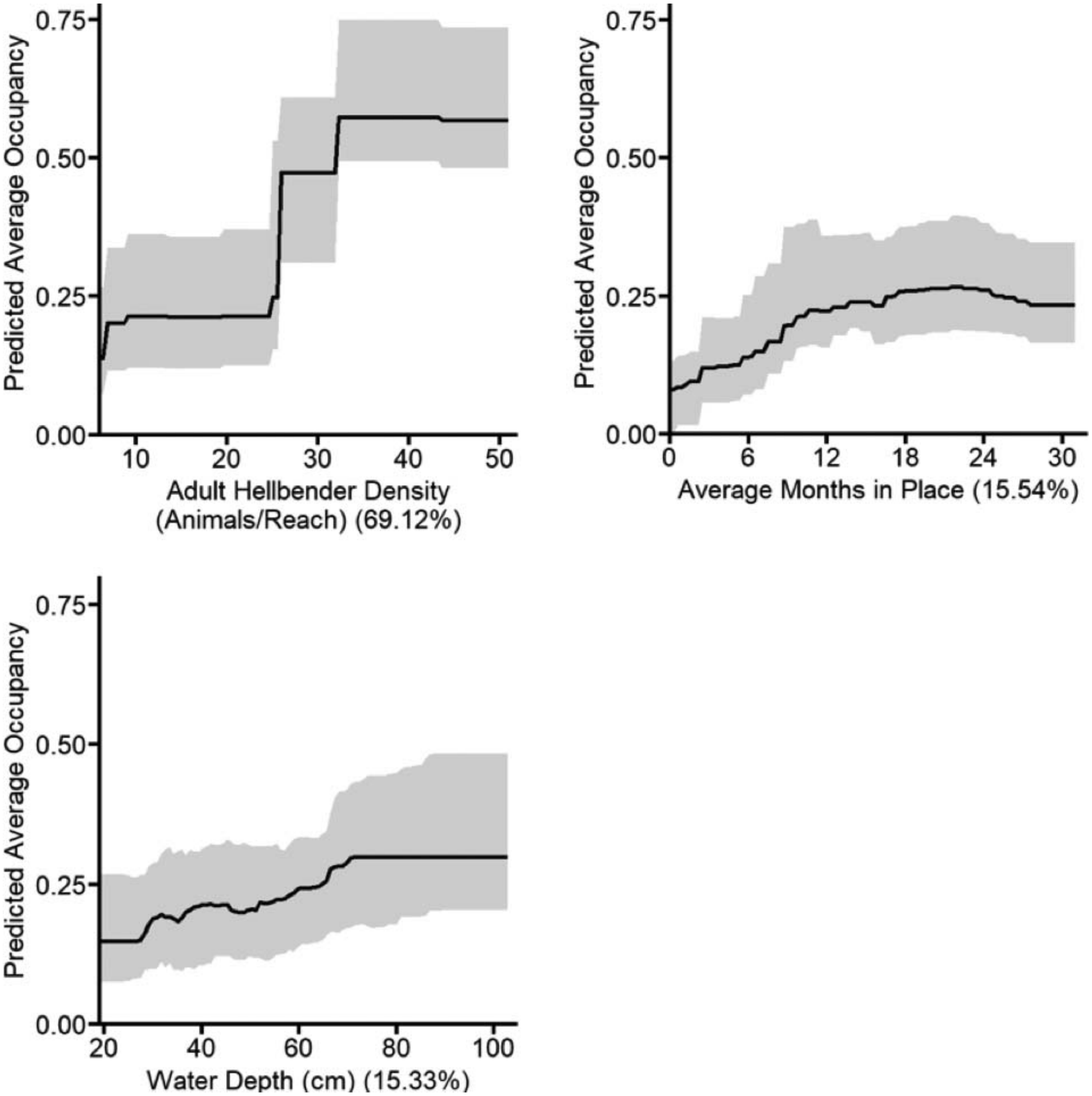

FIG. 1.—Partial dependence plots for the most important predictor variables retained in the final version of the selected model of shelter occupancy by Hellbenders (*Cryptobranchus alleganiensis*) in the Upper Tennessee River drainage. Solid black lines show fitted functions, whereas shaded areas represent 95% percentile–based confidence intervals built using 200 bootstraps. Numbers in parentheses on the x-axes indicate the percentage of influence of each predictor variable on the model's output. Values along the y-axes correspond with predicted average occupancy across all surveys of a given shelter.

habitat variables on shelter use consistent with other studies of resource use by stream-associated species (Thompson et al. 2001; Anderson et al. 2009), we compared the performance of BRTs that excluded 5 m and/or reach-scale predictors to those that included predictor variables from all spatial scales (Appendix S-IV, Supplemental Material). To ensure that the inclusion of data from single-year reaches did not weaken model performance, we also reevaluated the performance of our top model from the set using only data from our six multiyear study reaches with density estimates. Additionally, we reran our top occupancy and nesting model with shelter design as an added predictor variable, to determine whether a tradeoff existed between shelter stability and use.

RESULTS

Whereas Hellbenders did take up residence in the artificial shelters, shelter use varied widely across reaches. In total, Hellbenders occupied artificial shelters on 2518 of 6793 possible occasions (37%), with reach-scale occupancy averaging 22% (range ¼ 0–58%; percentage of occupancy summed across all shelters within a reach) across all surveys. With few exceptions, occupied shelters were used only by adult individuals. Average occupancy peaked at 26% approximately 2 yr after shelter deployment, and remained relatively constant thereafter (Fig. 1). Shelter occupancy increased most rapidly after shelter deployment in reaches containing high densities of adult/subadult Hellbenders

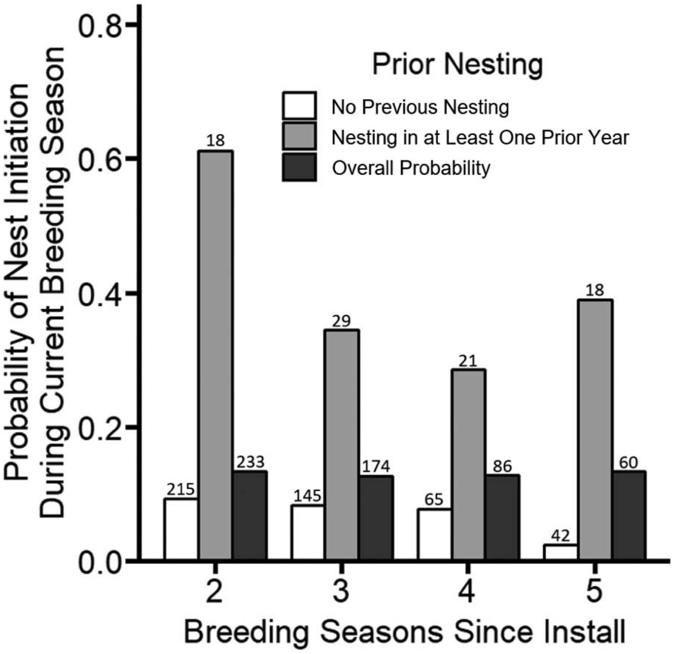

FIG. 2.—The influence of breeding seasons since installation and nesting by Hellbenders (*Cryptobranchus alleganiensis*) during prior breeding seasons on the probability of future nesting activity during a given breeding season, in the Upper Tennessee River drainage. Numbers above bars reflect sample sizes for each group.

(-1.5 individuals/100 m^2), but plateaued after 2 yr regardless of population density (Fig. 1).

Nesting in our artificial shelters by Hellbenders also varied widely across reaches. Hellbenders established nests in shelters on 95 of 925 nesting opportunities (10%; i.e., the summed number of breeding seasons that the shelters were collectively deployed), and reach-scale nest initiation averaged 8% (range¼0–18%) across all breeding seasons. These 95 nests were established in 61 different shelters, by 54 unique males. Prior nesting at a shelter substantially increased the probability of future nesting in that shelter (Fig. 2). Additionally, for shelters in place for multiple breeding seasons, 34% (25/73) that were used for nesting during a given breeding season were also used for nesting by the same male during the previous breeding season. Shelter design exerted , 2% influence on our top-performing models when added as a variable to them, indicating that design did not influence occupancy or nesting frequency.

Relationship Between Collective Habitat Variables and Shelter Use

The PERMANOVA and betadisper analyses revealed that the collective variance and average values of our two sets of predictor variables were related to both shelter occupancy (*F* ¼ 13.08, *P* ¼ 0.001, and *F* ¼ 4.20, *P* ¼ 0.001, respectively) and shelter nesting (*F* ¼ 2.29, *P* ¼ 0.015, and *F* ¼ 2.38, *P* ¼ 0.016, respectively). Moreover, whereas our PERMANOVA results should be interpreted with caution on account of the significance of our betadisper results (Oksanen et al. 2008); the betadisper results provided evidence of at least a moderate relationship between shelter use and the dispersion of ordinated predictor variables (Appendix S-II, Supplemental Material; *r*¼–0.25 between the response variable and the average distance of predictor variables from the overall centroid for average shelter occupancy, and *r* ¼ –0.48 for average shelter nesting). Therefore, we deemed our two sets of predictor variables appropriate for modeling the relationship between individual predictor variables and shelter use in subsequent BRTs.

Factors Influencing Shelter Occupancy

Our model built using variables from all three spatial scales, prior to dropping unimportant variables, had the highest performance among all models in the set (cross-validated correlation¼0.658, SE ¼0.043; Model A in Table 3), and outperformed other models that included predictor variables from two or fewer spatial scales (Table 3; Appendix S-IV, Supplemental Material). The top-performing model indicated that shelter occupancy depended primarily on the density of adult/subadult Hellbenders, and secondarily on average months since installation and water depth at the shelter's tunnel (Fig. 1). Other models in the set performed similarly, and retained a similar set of predictor variables. In the top model, shelter occupancy increased with hellbender density, with that variable being -4 times as influential as any other predictor variable on the model (69% relative influence; Fig. 1). Average months since installation and water depth were also positively associated with shelter occupancy to a lesser degree, and had relative influences of 16% and 15% on the model, respectively. Average shelter occupancy was only positively associated with time since shelter installation during the first 2 yr of shelter deployment, however, and increased most rapidly in reaches with high densities of adult/subadult Hellbenders (Fig. 3). The low contribution of shelter design when added to our top model (0.5%) indicated that it did not influence shelter occupancy. When all variables were optimized, predicted average occupancy reached 67%.

Factors Influencing Shelter Nesting

We constructed our top nesting model (cross-validated correlation ¼0.278, SE 0¼.042; Model A in Table 3) using predictor variables from all three spatial scales prior to dropping variables with minimal contributions. The top model explained up to 36% more variation in nesting than other models in the set (Table 3; Appendix S-IV, Supplemental Material), and retained water depth (44% influence), population density (34% influence), and the number of breeding seasons (22% influence) as important predictor variables. Predicted nesting frequency was greatest at water depths of approximately 50–60 cm, and increased with increasing densities of adult/subadult Hellbenders (Fig. 4). Average nesting frequency increased during the first three breeding seasons following shelter deployment, and plateaued thereafter. Unlike shelter occupancy, the rate of increase in shelter nesting over time following shelter deployment was unrelated to population density (Fig. 3). The relative influence of shelter design was negligible (2.4%) when added to our top model, suggesting that it did not substantially influence nesting frequency. When all variables were optimized, predicted average nesting frequency reached 24%.

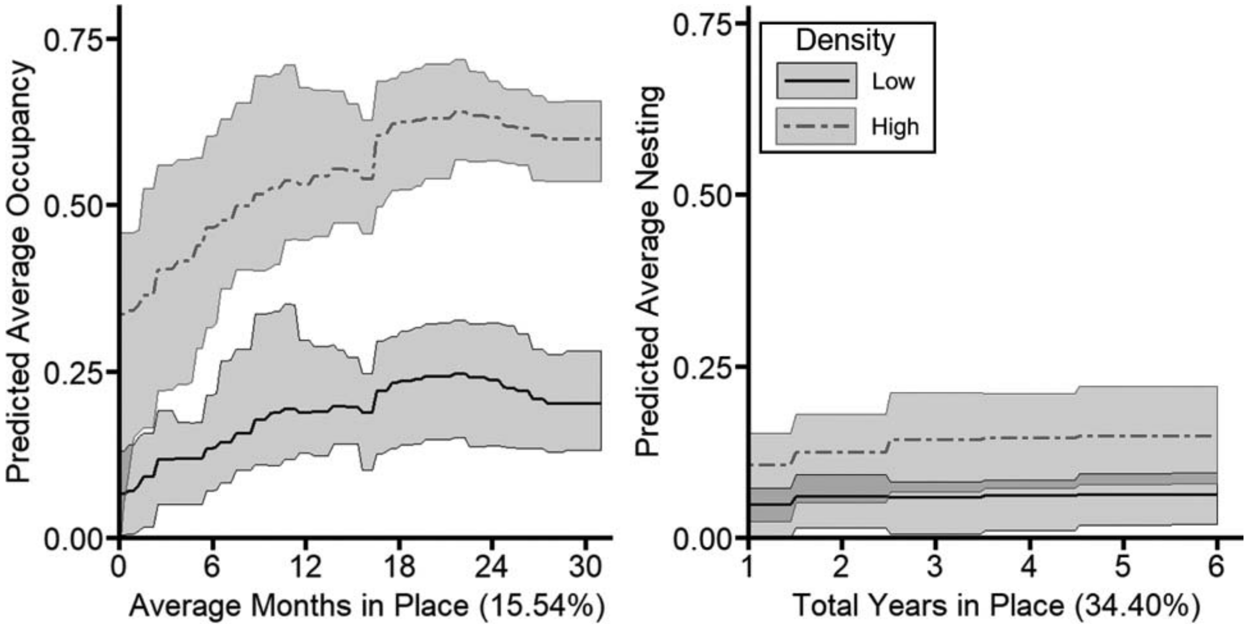

FIG. 3.—The influence of the density of adult/subadult Hellbenders (*Cryptobranchus alleganiensis*) on the relationship between time in place and shelter use in the Upper Tennessee River drainage. Density of Hellbenders was rated as high in reaches with ≥ 1.5 adult and subadult Hellbenders per 100 m^2, or otherwise low. Numbers in parentheses on the x-axes indicate the percentage of influence of each predictor variable on the model's output. Values along the y-axes correspond with predicted average occupancy or nesting across all surveys or breeding seasons in which the shelter was deployed.

DISCUSSION

We observed both occupancy and nesting activity by Hellbenders in our artificial shelters, which highlights the utility of these structures for monitoring this sensitive species. Moreover, because we detected an influence of three different variables on occupancy and nesting, only one of which was related to microhabitat features, our results indicate that, within our study system, optimizing shelter placement is a relatively simple process. Given the expected annual occupancy and nesting frequency in optimally placed artificial shelters in this system (up to 67% and 24% respectively), artificial shelters are a potentially powerful tool for monitoring populations of Hellbenders.

Shelter occupancy increased consistently with increasing density of Hellbenders across the reaches examined in our study (Fig. 4), but was influenced by water depth only at the microhabitat scale. Shelter occupancy exceeded 25% in low-density reaches (i.e., ≤ 1.0 subadult/adult individual per 100 m^2) within 2 yr of shelter deployment when shelters were deployed in optimal microhabitats (i.e., in portions of the stream ≥ 50 cm deep; Table 1). Deployed accordingly, shelter occupancy can improve within reaches where occupancy is otherwise limited by a low density of Hellbenders. This finding suggests that deeply placed artificial shelters might be effective for monitoring Hellbenders across a range of population densities, possibly because Hellbenders are seasonally reliant upon deep runs (Green 1934).

Regardless of where artificial shelters were placed, their occupancy by Hellbenders tended to increase in the first 2 yr following deployment. We attribute this result to the low vagility of Hellbenders (Topping and Peterson 1985; Peterson 1987; Blais 1996; Bodinof et al. 2012), and thus a gradual discovery of the additional habitat provided by artificial shelters. Studies of nest box use by birds and mammals have produced similar results, and have often documented periods of increasing use following artificial shelter installation, which eventually levels off or declines thereafter (McCamant and Bolen 1979; Katzner et al. 2005; Lindenmayer et al. 2009). Given a 2-yr shelter discovery period for Hellbenders, those shelters that were never occupied within 2 yr of deployment (even when deployed in suitable microhabitats) may have gone unused simply because they were not located within the core home range of any individual. Thus, these shelters had low discoverability even when placed in otherwise suitable locations. If the primary objective of shelter deployment is to maximize occupancy of shelters, we recommend relocating shelters that go unoccupied by Hellbenders for two or more consecutive years to improve their likelihood of future occupancy. Given the goal of maximizing shelter occupancy, relocation of shelters might be most beneficial in reaches with high densities of adult/subadult Hellbenders (cf. Fig. 3). Of course, relocating consistently unused shelters requires labor and produces habitat disturbance, so the utility of doing so will depend on project objectives and available resources.

Similar to Jachowski et al. (2020), we found that shelter occupancy increased concomitantly with the density of adult/subadult Hellbenders, and improved for 2 yr following shelter deployment. In contrast to their study, however, we found evidence of a positive relationship between natural shelter density and shelter occupancy by Hellbenders. This discrepancy is most likely attributable to a fundamental difference in how the two efforts assessed the abundance of natural shelters suitable for Hellbenders in a stream reach. Jachowski et al. (2020) considered all boulders (rocks ≥ 25.6 cm on the secondary axis) and all bedrock as natural shelter for Hellbenders, and found that boulder/bedrock density was generally negatively associated with artificial shelter occu-

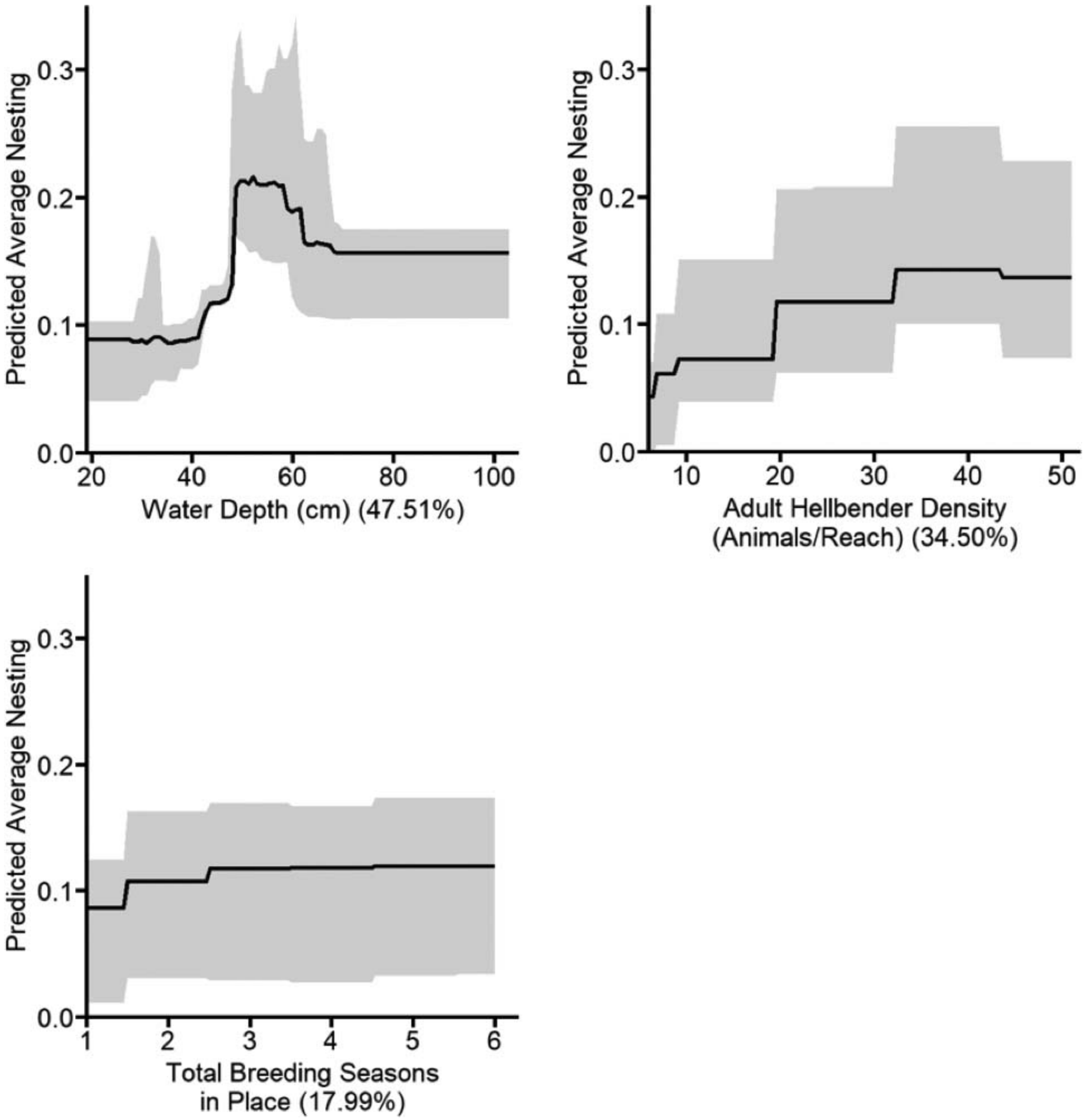

FIG. 4.—Partial dependence plots for the most important predictor variables retained in the final version of the top performing model of shelter nesting by Hellbenders (*Cryptobranchus alleganiensis*) in the Upper Tennessee River drainage. Solid lines show fitted functions, while shaded areas represent 95% percentile-based confidence intervals built using 200 bootstraps. Numbers in parentheses on the x-axes indicate the percentage of influence of each predictor variable on the model's output. Values along the y-axes correspond with predicted average nesting probability across all breeding seasons in which the shelter is deployed.

pancy. In contrast, we only included large boulders (≥ 40 cm on the primary axis) that bore suitable crevices in our estimates of appropriate habitat for Hellbenders. Unlike Jachowski et al. (2020), our metric assumed that all bedrock and boulder lacking suitable crevices were not suitable for Hellbenders. We suspect that our classification of suitable habitat, and possibly other differences in study design (i.e., inclusion/exclusion of different study reaches), explain this particular disparity between the two studies. Additional research is needed to understand the complex interplay among natural habitat availability, population density, and artificial shelter use by Hellbenders.

Nesting activity within shelters was related to similar factors as their occupancy, but the relative influence of these factors was more evenly partitioned (Fig. 4). Nesting was greatest in shelters located in moderately deep (50–60-cm) portions of the stream. Water depth was also nearly three times as important for predicting nesting frequency when compared to breeding seasons since shelter deployment (Fig. 4). Hellbenders might have perceived moderately deep runs as suitable for nesting because these areas featured cooler water than shallower areas (Kramer 1987). Additionally, Hellbenders might have perceived these deeper areas as being better protected from certain predators (e.g., wading birds) than shallow areas. Because shelter nesting was more than twice as high in moderately deep (50–60-cm) areas than in shallow (20–40-cm-deep) areas, we suggest that monitoring reproduction of Hellbenders will be more successful if shelters are placed in sufficiently deep water.

Based on our results, we provide three practical recommendations for future studies of Hellbenders that incorporate artificial shelters. First, expectations about shelter occupancy and nesting should be scaled according to the reach-wide density of adult/subadult Hellbenders, as shelter use was strongly influenced by this parameter. Secondly, shelters should be deployed in moderately deep locations (at least 50 cm deep in our study system), because doing so improved shelter occupancy and nesting regardless of the density of Hellbenders during our study. Finally, shelters not occupied within 2 yr of installation should be relocated to appropriate microhabitat in another part of the stream channel if the objective is to improve future occupancy, because shelter occupancy did not increase once shelters had already been in place for 2 yr.

Our study is the first to quantitatively evaluate patterns of artificial shelter use by Hellbenders over several (5+) years, and we are encouraged by the occupancy of individual shelters (22%) and the number of constructed nests (95). Habitat features not considered here, or found unimportant in our analyses, might yet be informative for shelter use by Hellbenders outside of our study region. As such, future studies should consider evaluating the applicability of our results to other populations of Hellbenders across the species' range, and assessing whether the relationship between shelter use and other variables not considered here (e.g., density of cobble, alternate shelter design; Mohammed et al. 2016) are equally important for shelter use by Hellbenders. For example, clustering of shelters within habitat patches known to be occupied by Hellbenders is a strategy used in other watersheds to maximize shelter occupancy (J. Briggler, personal communication). Provided that our results are applicable in other watersheds, we suggest that artificial shelters deployed in optimal locations can serve as novel, valuable tools for monitoring and conserving Hellbenders. Our study also serves as a template for using regularly maintained artificial shelters to examine other crevice-associated aquatic species that are secretive and/or of conservation concern (e.g., large crustaceans, certain fish species, and other salamanders).

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-19-00035.S1.

Acknowledgments.—We thank J. Kleopfer for his invaluable support throughout the study, the landowners who allowed us to access streams through their properties, and B. Brown and J. Snodgrass for their helpful feedback on this manuscript. We also thank J. Hallagan, H. Davie, J. Connock, C. Frazier, M. Lacey, T. Pirault, A. Grimaudo, V. Alaasam, J. Gomes Da Silva Neto, H. Vogel, G. Martin, and S. 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 US Fish and Wildlife Service. Additional funding was provided by the US Forest Service and a National Science Foundation grant (IOS-1755055). 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 (protocols 16-162, 13-128, 11-140, and 08-085).

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Accepted on 22 July 2020
Associate Editor: Michael Freake