# HERPETOLOGICA

## Movement and Habitat Use of Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) Following Population Augmentation

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ABSTRACT: With amphibian declines at crisis levels, translocations, including population augmentations, are commonly used for amphibian conservation. Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) have declined to low densities in many areas of their range, making them ideal candidates for population augmentation. Both wild adults and captive-reared juveniles have been used for augmentations, but their suitability has never been directly compared. Herein, we use radio telemetry with Eastern Hellbenders to examine patterns of site fidelity, movement, and habitat use over a 2-yr period for adult residents, wild adult translocates, and captive-reared juvenile translocates. We used generalized linear models and generalized linear mixed models to identify temporal trends and explore the effects of residential status (resident vs. translocate) and origin/age (captive-reared juveniles vs. wild adults) on various ecological and behavioral traits relating to habitat. Site fidelity was high in adult residents and wild adult translocates, but lower in captive-reared juvenile translocates. Both adult and juvenile translocates had greater mean movement distances than residents, leading to larger home range sizes, but these differences decreased over time. Wild adult translocates had a higher probability of using artificial nest rocks than adult residents or captive-reared juvenile translocates. This pattern was most prevalent early in the study, indicating these shelters are particularly useful during the transition to release sites. Captive-reared juvenile translocates had lower site fidelity and utilized suboptimal habitat (smaller and fewer shelter rocks) compared to wild adults. Compared to previous studies, translocations had fewer negative effects on site residents or wild translocates and might be effective at promoting growth of Hellbender populations. However, translocations of captive-reared juveniles were less successful. As we are uncertain whether captive-rearing or ontogeny led to these differences, both longer head-starting times and conditioning should be explored to improve outcomes in captive-reared juvenile cohorts.

Key words: Caudata; Home range; Radio-telemetry; Salamander; Translocation

GLOBAL amphibian declines have reached crisis levels, with approximately one-third of recognized species facing extinction (Zippel and Mendelson 2008). Translocations, the intentional movement of organisms from one area to another, represent a potential conservation action to reverse current trends (Armstrong and Seddon 2008). Although the usefulness of translocations for amphibians has been called into question (e.g., Dodd and Seigel 1991; Tapley et al. 2015), recent studies have suggested that both the prevalence and the success of amphibian translocations have increased over time, and such strategies are now considered a priority action for amphibian conservation (e.g., Griffiths et al. 2007; Griffiths and Pavajeau 2008; Germano and Bishop 2009). Reintroductions, a type of translocation where animals are moved into parts of their range where they were historically extirpated, comprise the majority of amphibian translocations, but population augmentations can also be useful for combating amphibian declines (Germano and Bishop 2009; Ewen et al. 2014). Augmentations, which involve moving animals to increase local populations, are used to speed population growth, overcome dispersal barriers, and/or increase the genetic diversity of a population (Seddon et al. 2012). However, augmentations can only be effective if translocated animals settle and establish home ranges within release sites (Le Gouar et al.

2012). Furthermore, unlike reintroductions, the welfare of existing residents is a concern following augmentations (Griffiths et al. 2007). Postrelease monitoring is essential to demonstrate the effectiveness of the technique as a management tool and ensure the well-being of all members of the population.

Quantifying postrelease survival is an important first step for assessing the success of translocations, but it does little to distinguish among the causes of success or failure (Seddon et al. 2012). Monitoring postrelease movement and habitat use might help fill in these knowledge gaps. Long-distance dispersal from translocation sites is associated with reduced survival and reproductive success in released individuals (Stamps and Swaisgood 2007; Le Gouar et al. 2012) and is the most common cause of translocation failures in herpetofauna (Germano and Bishop 2009). Long-distance dispersals from release sites often occur during a postrelease exploratory phase in which released individuals examine their new environment (Le Gouar et al. 2012). This stage is associated with a higher frequency of movement and/or greater movement distances, resulting in a larger home range size (Berger-Tal and Saltz 2014). A prolonged exploratory phase can be detrimental to postrelease survival and reproductive success, as the energy required for movement reduces the energy available for foraging or reproduction (Le Gouar et al. 2012). Additionally, translocation of wild individuals can result in long-distance

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dispersal from translocation sites attributable to homing behavior (Germano and Bishop 2009). Observing postrelease habitat use is also a useful monitoring tool, because postrelease habitat selection is often linked to translocation success (Le Gouar et al. 2012). Temporal factors, such as time since release and season, can further complicate postrelease patterns of movement and habitat use (Le Gouar et al. 2012). The origin (captive-reared vs. wild), age, and sex of individuals might also influence these patterns, and thus, the ultimate success of translocations and augmentations (Le Gouar et al. 2012). A thorough understanding of the general patterns of movement and habitat use at release sites, as well as the temporal progression of these patterns, can provide valuable insight into the long-term consequences of management actions.

Translocation is one of the tools currently used to aid in the conservation of Hellbenders (*Cryptobranchus alleganiensis*; Briggler et al. 2010; Williams et al. 2013). Hellbenders are large, aquatic salamanders found in highly oxygenated lotic systems (Mayasich et al. 2003). The Ozark subspecies (*Cryptobranchus alleganiensis bishopi*) is currently listed as endangered (Gould 2011), and the eastern subspecies (*Cryptobranchus alleganiensis alleganiensis*) is threatened throughout much of its range (Mayasich et al. 2003). Hellbenders spend the majority of their time alone under large, flat rocks that they will defend from conspecifics (Nickerson and Mays 1973; Peterson and Wilkinson 1996). Adults tend to be sedentary with small home ranges, although there are sometimes seasonal bursts of movement attributable to breeding activity (Petranka 1998; Burgmeier 2011a). Although several studies have examined the movement patterns and habitat use of translocated Hellbenders (Bodinof et al. 2012a; Boerner 2014), none have directly compared these measures in translocates and residents at augmentation sites, or focused on the effect of augmentations on residents.

Historically, both wild adults (Gates et al. 1985) and captive-reared juveniles have been used as a source for Hellbender translocations (Bodinof et al. 2012a; Boerner 2014). Captive-reared juveniles are sourced from clutches that are collected in the field, hatched in a laboratory setting, and reared until hatched in a laboratory setting and reared until they are large enough to avoid many sources of larval mortality (usually after 3–5 yr in captivity; Bodinof et al. 2012a; Boerner 2014). Sexual maturity occurs at 5–6 yr in Hellbenders (Bishop 1941), so captive-reared juveniles are often released prior to reaching sexual maturity. If the purpose of augmentations is to encourage reproduction, using wild adult translocates from isolated sites within the same watershed might produce faster results than using captive-reared juveniles, because they are already sexually mature and potentially available for breeding. This approach can be problematic if animals attempt to return to their collection site, however, and strong homing behavior has been demonstrated in adult Hellbenders (Hillis and Bellis 1971; Gates et al. 1985; Blais 1996). Captive-reared juveniles have shown potential as translocates (Bodinof et al. 2012b), but a lack of conditioning might leave them unprepared for their new environment (Stamps and Swaisgood 2007; Kenison and Williams 2018). Investigating the differences in postaugmentation movement and habitat use patterns in

the two groups can help formulate management recommendations for future translocations.

In Indiana, Eastern Hellbenders are restricted to a single river with densities reduced by two orders of magnitude over a 25-yr period (Burgmeier et al. 2011c). Although the original causes of decline are unclear (Burgmeier et al. 2011b), current recruitment failure is likely exacerbated by limited mating opportunities attributable to the low population density. Individuals in the river are patchily distributed in fragments of suitable habitat, which often results in isolation (Burgmeier et al. 2011c). Augmentations in this population were undertaken with the expectation that increasing local densities could potentially encourage reproduction and provide a source of egg masses for future captive-rearing efforts (Williams et al. 2015). We also installed artificial nest rocks (ANRs; Briggler and Ackerson 2012) to aid in egg collection efforts by providing easily accessible nest sites, and to potentially supplement the Hellbender habitat during the nonbreeding seasons.

To explore the potential utility of both population augmentation and habitat supplementation for future conservation efforts involving Hellbenders, we radio-tagged and monitored adult residents, wild adult translocates, and captive-reared juvenile translocates over a 2-yr period. Kraus et al. (2017) found that survival rates were generally high in both adult residents and wild adult translocates but were lower in the captive-reared juvenile cohort. To try to understand these trends, as well as elucidate more subtle differences that did not immediately contribute to survival rates, we examined patterns of site fidelity, movement, and habitat use. We then used a series of generalized linear models (GLM) and generalized linear mixed models (GLMM) to examine temporal trends in the data and explore the effects of a series of covariates including residential status (resident vs. translocate), origin/age (captive-reared juvenile vs. wild adult), and sex (male vs. female) on movement probability, movement distance, home range size, shelter rock size, number of adjacent shelter rocks, and probability of artificial nest rock use. For our movement models, we also included data from individuals collected for a baseline movement study (Burgmeier et al. 2011a), to determine whether or not our management actions (i.e., population augmentation and habitat supplementation) affected overall movement patterns at managed sites compared to unmanaged sites.

MATERIALS AND METHODS

Study Area and Site Selection

The study area encompasses a 112-km portion of the Blue River in southern Indiana and covers the range of historical locations of Eastern Hellbenders recorded within the system (Kern 1984). The Blue River is a tributary of the Ohio River that originates in Washington County and flows southward through Harrison and Crawford counties. The Blue River is an entrenched river bordered by a mosaic of agricultural fields and forest habitat. The substrate is largely gravel and cobble with sections of bare bedrock (Burgmeier et al. 2011b), but there is substantial sedimentation within the system (personal observations). Like many rivers in which Eastern Hellbenders are found (Nickerson and Mays 1973), appropriate habitat consisting of dense groups of boulders is patchily distributed

throughout the river. Two translocation sites within the river were selected based on habitat features available within the sites. Both sites consisted of approximately 500 linear meters of dense boulder habitat directly preceded or followed by less suitable matrix habitats with gravel or sand substrates and patchily distributed boulder habitat. The sites represented two of the most contiguous patches of boulder habitat within the study area and had the greatest density of Hellbenders among the 42 sites sampled during a previous population monitoring study (Burgmeier et al. 2011c).

## Field Methods

The translocation study took place from 2011 to 2013. We followed 11 adult residents and 11 wild adult translocates at Site 1. At Site 2, we followed 10 adult residents and 10 captive-reared juvenile translocates. As with other Hellbender populations in decline (Nickerson et al. 2003; Foster et al. 2009), populations in Indiana are biased towards adults (Burgmeier et al. 2011c); thus, all captured site residents and translocates were large adults. Technically, the captive-reared individuals were all large enough to be considered adults (with total length [TL] >30 cm in all subjects at the time of release; Peterson et al. 1983; Hopkins and DuRant 2011). However, there was a difference in the ages of the two cohorts since  there was no overlap in the size class of wild individuals (42.8–58.0 cm TL) and captive-reared individuals (34.5–38.4 cm TL). This makes it impossible to distinguish whether differences in movement or habitat use are because of origin (i.e., captive-reared vs. wild) or ontogeny (i.e., adult vs. juvenile); however, these two size classes represent the groups that are likely to serve as Hellbender translocation sources. All subjects had a staggered entry into the study, with residents entering the study prior to translocates. Individual release dates are detailed in Kraus et al. (2017).

Site residents and wild translocates were captured by hand or net through rock lifting surveys (Browne et al. 2011). Upon capture, we recorded the total length (cm), snout–vent length (SVL; cm), and mass (g) of all individuals. Translocated individuals were moved from low-density sites (they were often the only individual present within an isolated site) located throughout the Blue River. We conducted surgeries immediately upon capture for all resident Hellbenders. Translocated adults were transported to Site 1 prior to surgery (Kenison et al. 2016). All captured residents and translocates were adults between 422 and 1218 g ($\bar{X} \pm 1$ SE $= 716 \pm 33$ g). They were implanted with a 13 g, $50 \times 11$–mm transmitter with whip antenna (SI-2 model; Holohil Systems, Ltd.) following Burgmeier et al. (2011a). All wild adults were sexed via cloacal swelling during the breeding season. The majority of wild, adult Hellbenders were released in June and July 2011 (Kraus et al. 2017).

Because this study occurred prior to the establishment of a captive-rearing program in Indiana, the translocated juvenile Hellbenders were sourced from a single clutch of eggs collected from Buffalo Creek in West Virginia, USA during September 2007. Previous work suggested that Hellbenders from West Virginia could serve as a suitable genetic source population for Indiana translocations (e.g., Unger et al. 2013). The eggs were transported and hatched at the Fort Worth Zoo, in Texas, USA. We moved 18 captive-reared juveniles to the Purdue Aquaculture Research Laboratory, in West Lafayette, Indiana, USA, during June

2011 and monitored their growth for 14 mo. In September 2012, the 10 largest individuals were examined by laparoscope to determine their sex prior to being implanted with radio transmitters (Gentz 2007). Three of the larger individuals (weighing between 243 and 297 g) were implanted with the same model radio transmitters as the adult Hellbenders. We implanted each of the remaining seven juveniles, who weighed between 158 and 240 g ($\bar{X} = 197 \pm 10$ g), with a 9 g, $33 \times 11$–mm transmitter with whip antenna (also SI-2 model). The juveniles were held within captivity for an additional month to ensure appropriate healing of the surgery sites and then, October 2012, transported to their release site (Kenison et al. 2016). Additional details on the captive-rearing protocol are available in Kraus et al. (2017).

At both sites, the habitat was augmented prior to the beginning of the study with the addition of 15 artificial nest rocks (Briggler and Ackerson 2012). Following their installation, artificial nest rocks (ANRs) were rinsed to remove sediment and repositioned on an annual basis. All individuals were placed in soft-release enclosures within the translocation site for 48–60 h to minimize initial dispersal. Kraus et al. (2017) provide the details of the soft release enclosure construction. Residents were released underneath their original capture rock and wild adult translocates were individually released under ANRs. Captive-reared juveniles were released under ANRs in pairs. Following release, Hellbenders were tracked with a two-element H antenna coupled to a TRW-1000 receiver (Wildlife Materials, Inc.). Individuals were tracked to their shelter rocks unless river conditions were deemed unsafe for tracking (above 1 m at the nearest gage), in which case individuals were tracked from the bank and simply recorded as being within or outside of the study site. Shelter rocks were marked between observations, and we noted the movement of individuals to new shelter rocks. Upon the first observation at a shelter rock, we recorded the location with a global positioning system (GPS) unit (Rino 110, Garmin; resolution $\pm$ 4 m, datum = NAD83). Along with subject location, habitat measurements including shelter rock size (length [cm] $\times$ width [cm]) and the number of surrounding shelter rocks (those >25.6 cm in diameter and within a 6-m radius of subject location) were collected. We also recorded whether the subject was occupying an ANR. We tracked individuals 2–3 times weekly from June–November, and at least monthly during the rest of the year. Individuals were tracked until August 2013 unless they died, disappeared from the study area, or were subject to transmitter failure prior to that date.

## Fidelity, Movement, and Habitat Metrics

All field locations were recorded in a geodatabase layer and, unless otherwise noted, visualized using ArcGIS (v10.2.2, ESRI, Redlands, CA). We used all available locations to calculate dispersal distance and proportion of downstream dispersals. For the remainder of the metrics, we were interested in quantifying temporal trends and truncated the data to include points taken only during June–November of 2011 and 2012 because we collected data most regularly during those time periods. One translocated adult individual was removed from the calculation of all metrics, because it remained in the study for only 7 d. We report the results of all calculated metrics as means $\pm$ 1 SE.

TABLE 1.—Summary of all models used to examine trends in movement patterns and habitat use in resident and translocated Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) at two sites in the Blue River in Indiana.

| Dependent variable | Distribution | Random effects | Full model fixed effects |
| --- | --- | --- | --- |
| Movement probability | Binomial | ID, site | Days since last observation + days since release + management + origin/age + residential status + season + sex |
| Movement distance | Negative binomial | ID, site | Days since last observation + days since release + management + origin/age + residential status + season + sex |
| Linear home range | Negative binomial | | Number of observations + management + origin/age + residential status + sex |
| Mean convex polygon home range | Negative binomial | | Number of observations + management + origin/age + residential status + sex |
| Monthly linear home range | Negative binomial | ID, site | Months since release + number of observations + origin/age + residential status + season + sex |
| Shelter rock size | Negative binomial | ID | Days since release + origin/age + residential status + season + sex + site |
| Number of Surrounding shelter rocks | Negative binomial | ID | Days since release + origin/age + residential status + season + sex + site |
| Artificial nest rock use probability | Binomial | ID | Days since release + origin/age + residential status + season + sex + site |

We quantified site fidelity by counting the number of individuals in each group (wild adult translocates, wild adult residents, and captive-reared juveniles) that remained within the translocation site at the end of their time in the study. We calculated the percentage of individuals displaying high site fidelity by dividing the number of individuals whose final location was <4 m of the study site by the total number of individuals in each cohort. To quantify dispersal distance, we measured the maximum distance that each subject moved upstream and downstream from its point of release. The larger of the two values was assigned as dispersal distance and used to separate individuals into upstream or downstream dispersal categories. We averaged the larger of the values over all individuals to determine mean dispersal distance.

To explore general movement patterns, we calculated mean movement probabilities, mean movement distances, and multiple home range estimates for each individual. We calculated the overall probability of movement between successive observations for each of the telemetered Hellbenders by dividing the total number of movements by the total number of observations for that subject. To calculate mean movement distances, we calculated the distance (m) between all successive locations using the distGeo function (Hijmans et al. 2012) in R (v3.02; R Development Core Team 2013). We included only movement events in our calculation of the mean.

We calculated linear home ranges (LHR) and mean convex polygon (MCP) home ranges for each subject. The linear home range was calculated as the distance between the most upstream and downstream recorded location for that subject (Daugherty and Sutton 2005). MCPs were calculated as convex hulls containing all locations and with no interior angle exceeding 180 degrees (Mohr 1947). We used MCPs because of the difficulties associated with bandwidth selection with kernel density estimators, particularly in studies involving herpetofauna and anisotropic (i.e., directional) habitats (Row and Blouin-Demers 2006; Kie et al. 2010). To examine potential changes in home ranges over time in our translocation sites, we also calculated monthly LHRs for each individual in our study. We considered any movements >500 m between observations to be long-distance dispersal events and did not

include these locations in our home range calculations to avoid upwardly biasing the results. All calculated distances and home ranges were viewed within the ArcGIS environment, layered over aerial imagery (NAIP Best Available Imagery 2005–2011), and manually corrected when these parameters included areas outside of the river (Burgmeier et al. 2011a). We used mean shelter rock size, number of surrounding shelter rocks, and probability of ANR use to quantify habitat use. The probability of ANR use was calculated for each subject by dividing the number of times the individual was observed within an ANR by the total number of observations.

### Statistical Analyses

All statistical analyses were conducted in R (v3.02; R Development Core Team 2013) using generalized linear models (GLM) and generalized linear mixed models (GLMM) to examine the effects of covariates on movement and habitat variables. To examine the effects of augmentation on the movement patterns of site residents, we included data from a previous movement study within our movement probability, movement distance, LHR, and MCP home range analyses (Burgmeier et al. 2011a). The study used a very similar methodology and tracked 21 resident individuals at eight sites (1–4 individuals per site) throughout the Blue River during 2008 and 2009. This allowed us to compare movement metrics at managed sites (those with population augmentation and habitat supplementation) and unmanaged sites. We modeled movement probability by coding each successive location as a movement (1) or a nonmovement (0). We modeled monthly LHR sizes using only individuals from Site 1 because captive-reared translocates were added later in the study than adults. Habitat analyses only included data from the current study, because the addition of ANRs could have altered habitat use patterns. We modeled the probability of ANR use by coding each successive observation as ANR use (1) or nonuse (0). The resulting models for each of the dependent variables were based on different distributions and combinations of random and fixed effects (Table 1).

To explore temporal trends in our data, we included the covariates time since release and season whenever models were performed on longitudinal data (Table 2). We divided

Table 2.—Independent variables used in a series of models examining movement patterns and habitat use in Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) at two sites in the Blue River in Indiana.

| Variable | Description | Type |
|---|---|---|
| Days since last observation | Number of days since the last location point was recorded | Continuous |
| Days since release | Number of days since entry in the study | Continuous |
| Management | Premanagement (2008–2009) = 0, postmanagement (2011–2012) = 1 | Categorical |
| Months since release | Number of months since entry in the study | Continuous |
| Number of observations | Total number of location points recorded for an individual | Continuous |
| Origin/age | Captive-reared juvenile = 0, wild adult = 1 | Categorical |
| Resident status | Translocate = 0, resident = 1 | Categorical |
| Season | Summer (June, July, August) = 0, fall (September, October, November) = 1 | Categorical |
| Sex | Male = 0, Female = 1 | Categorical |
| Site | Site 1 = 0, Site 2 = 1 | Categorical |

our study period into summer (June, July, and August) and autumn (September, October, November) which corresponds roughly with the nonbreeding (summer) and breeding (autumn) seasons in Indiana (Burgmeier et al. 2011a). When necessary, we included control variables to account for total number of observations or the time between observations (Table 2). To examine differences between residents and translocated individuals, we included a covariate for residential status. We assessed demographic differences by including covariates for origin/age (wild adults vs. captive-reared juveniles) and sex (Table 2). We included a covariate for management to determine whether baseline movement patterns were different in sites where population augmentation and habitat supplementation occurred. All continuous independent variables were standardized to make model coefficients comparable.

When we had repeated measures of individuals, we specified individual as a random effect and fit models with a Laplace approximation with the use of package lme4 (Bates et al. 2014). We treated site as a random effect to account for potential variation between sites in movement models (because there were 10 individual sites, and we were not interested in the specific effects of each), unless the inclusion prevented model convergence (this only occurred in the LHR and MCP models). If both random effects were included within a model, they were treated as individuals nested within sites. Individuals and sites were removed from GLMMs if they did not have at least four repeated measurements. Because habitat data were collected only at the two translocation sites, we included site as a fixed effect within the three habitat models (shelter rock size, number of surrounding shelter rocks, and ANR use probability).

We used backward selection to fit the final models, first fitting models with all fixed effects and removing single

variables until all variables were significant ($\alpha < 0.05$) according to Wald's Z-tests (Bolker et al. 2009). We did not include interaction terms in our full models. We used the rsquared function to calculate conditional, marginal, and pseudo $R^2$ values for final models (Lefcheck 2015). We tested the assumptions associated with each statistical analysis utilized and assessed the fit of all final models.

## Results

During summer and autumn of 2011 and 2012, we recorded 4182 observations of our subjects. Site fidelity was high (88%), with 37 out of 42 final observations of individuals occurring within release sites. Adult residents had the highest site fidelity (100%), followed by wild adult translocates (90%), and captive-reared juvenile translocates (60%). Adult residents were more likely to disperse upstream (14/21), and wild adult translocates were equally likely to disperse upstream or downstream (5/10). All captive-reared juvenile translocates dispersed downstream (10/10). The mean dispersal distance for all individuals was 215.3 ± 36.9 m (Fig. 1). We observed five long-distance dispersal events in our study (>500 m movement from the release site). Three occurred in captive-reared juvenile translocates that did not return to the study site. One occurred in a wild translocate that moved steadily upstream before disappearing from the site. The final occurred in a site resident that moved upstream during the breeding season and remained at the upstream site for approximately 7 d before returning to the translocation site.

The mean movement probability for all individuals was 0.12 ± 0.01 and, when individuals did move, their displacement averaged 55.73 ± 9.19 m. The mean total LHR for all individuals was 260.25 ± 39.54 m, and the mean total MCP for all individuals was 7904.83 ± 2151.85 m². The

Table 3.—Model summaries for all final models related to movement patterns in resident and translocated Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) at two sites in the Blue River in Indiana.

| Movement variables | $R^2$ | Fixed effects | df | Estimate | SE | Z | P |
|---|---|---|---|---|---|---|---|
| Probability of movement | 0.08 (marginal) | Intercept | 1, 5150 | −2.10 | 0.31 | −5.88 | <0.001 |
| | 0.14 (conditional) | Days since last observation | 1, 5150 | 0.33 | 0.03 | 9.70 | <0.001 |
| | | Days since release | 1, 5150 | −0.23 | 0.05 | −4.92 | <0.001 |
| | | Management | 1, 5150 | −0.61 | 0.17 | −3.59 | <0.001 |
| | | Origin/age | 1, 5150 | 0.67 | 0.26 | 2.55 | 0.01 |
| | | Season | 1, 5150 | 0.18 | 0.09 | 2.11 | 0.035 |
| Movement distance | 0.34 (marginal) | Intercept | 1, 780 | 3.00 | 0.10 | 29.78 | <0.001 |
| | 0.90 (conditional) | Days since last observation | 1, 780 | 0.10 | 0.04 | 2.74 | 0.006 |
| | | Residential status | 1, 780 | −0.53 | 0.17 | 3.15 | 0.002 |
| | | Season | 1, 780 | 0.64 | 0.08 | 7.94 | <0.001 |
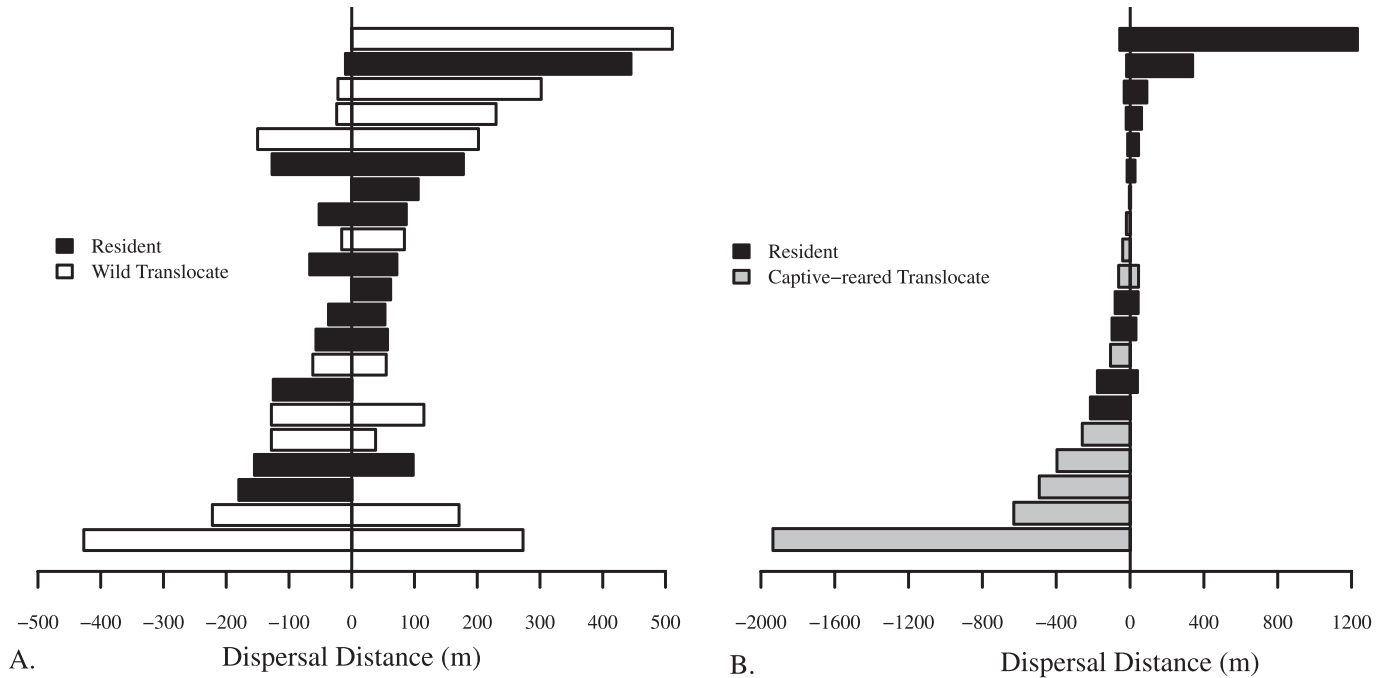
Fɪɢ. 1.—Dispersal distances of Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) in the Blue River in Indiana. Zero represents the point of release, positive values reflect upstream movements, and negative values reflect downstream movements. (A) Resident and wild translocated subjects at Site 1; (B) resident and captive-reared translocated subjects at Site 2.

mean monthly LHR for all individuals was 57.89 ± 13.08 m. Temporal factors influenced movement patterns. The probability of movement decreased with increasing time in the study, although movement distances did not (Table 3). This change in movement probability led to decreasing linear home range sizes over time (Table 4). Season had a significant effect in all movement models in which it was included (Table 3). Compared to summer, Hellbenders in autumn had a slightly higher probability of movement and a substantial increase in movement distances (Table 3), leading to larger home ranges in that season (Table 4).

Our management efforts (population augmentation and habitat supplementation) had a limited effect on the movement patterns of individuals, with only movement probability being affected. We saw a lower probability of movement in residents at our translocation sites (0.12 ± 0.01, $n = 21$) compared to residents in our unmanaged sites (0.28 ± 0.03, $n = 21$) even after controlling for the number of days between observations (Table 3). The mean movement distance was similar between residents at managed sites (29.45 ± 3.39 m, $n = 21$) and unmanaged sites (39.28 ± 5.79 m, $n = 21$). Likewise, both full LHR and MCP sizes were similar in residents in our previous study and those in our

current study. We did not compare differences in the monthly LHR size or habitat use before and after management.

Translocates moved greater distances than residents and thus had larger home range sizes. Translocates had the same movement probability as residents at 0.12 ± 0.01 ($n = 20$), but they moved greater distances than residents with a mean movement distance of 72.5 ± 16.8 m ($n = 20$; Table 3). These greater movement distances led to both larger total LHR (Fig. 2A) and MCP (Fig. 2B) sizes in translocates ($n = 20$) compared to residents ($n = 21$; Table 4), although the magnitude of the differences decreased over time (Fig. 3). Captive-reared juveniles displayed lower movement probabilities (0.09 ± 0.02, $n = 10$) than wild adults (0.13± 0.01, $n = 31$; Table 3), but there were no differences in movement distances (Table 3), LHR size (Table 4), or MCP size (Table 4). We saw no evidence of sex as a driver of movement patterns within our study.

The mean shelter rock size for all observations was 9376.0 ± 109.1 cm$^2$ and the mean number of surrounding shelter rocks was 62.0 ± 0.84. Individuals used less sheltered areas over time and used smaller, less sheltered boulders during the breeding season (Table 5). Captive-reared juveniles used smaller boulders (5449.4 ± 178.0 cm$^2$, $n = 10$) than wild

TABLE 4.—Model summaries for all final models related to home range size in resident and translocated Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) at two sites in the Blue River in Indiana.

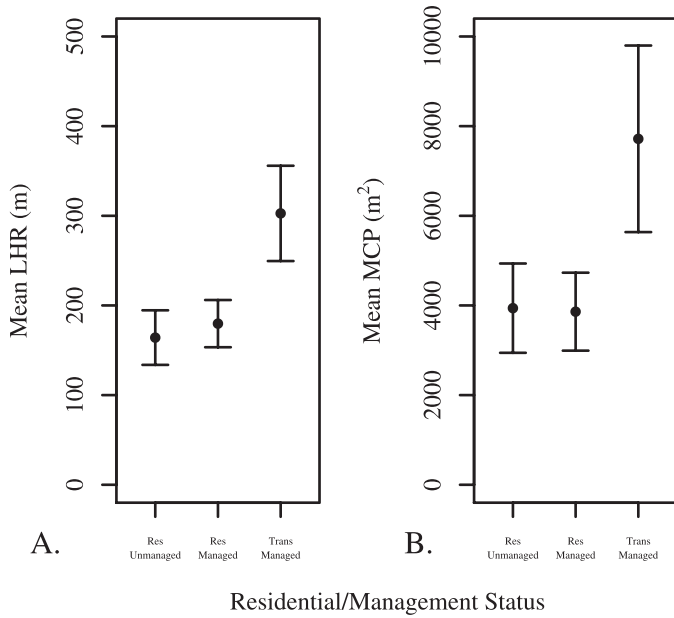| Home range variables | $R^2$ | Fixed effects | df | Estimate | SE | Z | P |
|---|---|---|---|---|---|---|---|
| Linear home range | 0.08 (pseudo) | Intercept | 1, 60 | 5.14 | 0.13 | 39.78 | <0.001 |
| | | Residential status | 1, 60 | −0.56 | 0.23 | 2.49 | 0.013 |
| Mean convex polygon | 0.06 (pseudo) | Intercept | 1, 60 | 8.26 | 0.18 | 46.85 | <0.001 |
| | | Residential status | 1, 60 | −0.68 | 0.31 | 2.20 | 0.028 |

Fig. 2.—(A) Mean size (±1 SE) of linear home ranges (LHR; [A]) and minimum convex polygon (MCP; [B]) home range size of resident (Res) and translocated (Trans) Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) at two sites in the Blue River in Indiana following population augmentation.

Fig. 3.—Mean monthly linear home range size (±1 SE) of resident and translocated adult Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) at two sites in the Blue River in Indiana over four seasons following population augmentation.

adults (9749.6 ± 115.7 cm², *n* = 31). Captive-reared juveniles also used boulders with less surrounding cover (54.7 ± 1.6) than wild adults (62.8 ± 0.8). The only habitat variable where sex was a factor was number of adjacent shelter rocks (Table 5). Females used more sheltered areas (70.7 ± 1.1 surrounding shelter rocks; *n* = 16) compared to males (54.4 ± 1.0 surrounding shelter rocks; *n* = 25). The mean probability of ANR use for all Hellbenders in the study was 0.11 ± 0.027. Hellbenders were more likely to use ANRs early in the study and during the breeding season (Table 5). Wild translocates (*n* = 10) had the highest probability of ANR use among all cohorts and captive-reared translocates (*n* = 10) had the lowest (Fig. 4C).

## DISCUSSION

The high rate of site fidelity and low mean dispersal distance in this study was unexpected given the results of previous translocation studies involving Hellbenders (Gates
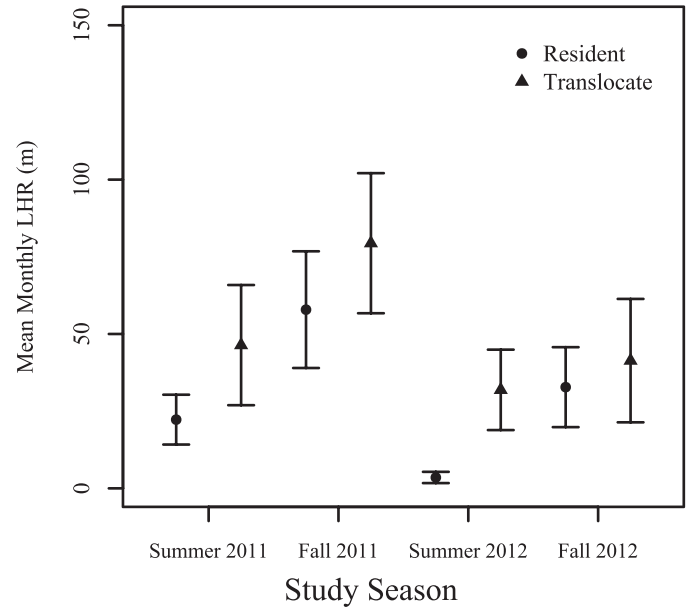
et al. 1985; Bodinof et al. 2012a; Boerner 2014), and they likely contributed to the high overall survival rates (Kraus et al. 2017). The mean dispersal distance of 215 m was also low compared to previous translocation studies that saw mean dispersal distances of 653 m in captive-reared juveniles (Boerner 2014) and 1026 m in wild adults (Gates et al. 1985). Low initial site densities might have played a role in the high levels of site fidelity by decreasing potential competition between residents and translocates. Although we increased the number of Hellbenders at both release sites (Burgmeier et al. 2011c), final site densities were still well below historic densities (Kern 1984). We observed only one homing attempt in the wild translocated cohort despite several studies demonstrating strong homing behavior in Hellbenders (Hillis and Bellis 1971; Gates et al. 1985; Blais 1996). Large release numbers have been correlated with success in herpetofauna translocations (Germano and Bishop 2009); however, releasing too many individuals into limited habitat has been shown to increase homing activity in salamanders

TABLE 5.—Model summaries for all final models related to habitat use in resident and translocated Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) at two sites in the Blue River in Indiana.

| Habitat variables | $R^2$ | Fixed effects | df | Estimate | SE | Z | P |
|---|---|---|---|---|---|---|---|
| Shelter rock size | 0.15 (marginal) | Intercept | 1, 2883 | 8.38 | 0.17 | 49.54 | <0.001 |
| | 0.99 (conditional) | Origin/age | 1, 2883 | 0.69 | 0.19 | 3.68 | <0.001 |
| | | Season | 1, 2883 | −0.06 | 0.02 | −3.02 | 0.002 |
| Number of adjacent shelter rocks | 0.33 (marginal) | Intercept | 1, 2620 | 3.49 | 0.17 | 19.99 | <0.001 |
| | 0.94 (conditional) | Days since release | 1, 2620 | −0.27 | 0.01 | −25.38 | <0.001 |
| | | Origin/age | 1, 2620 | 0.53 | 0.18 | 3.00 | 0.002 |
| | | Season | 1, 2620 | −0.20 | 0.02 | −10.58 | <0.001 |
| | | Sex | 1, 2620 | 0.31 | 0.14 | 2.16 | 0.030 |
| Probability of artificial nest rock use | 0.18 (marginal) | Intercept | 1, 4184 | −10.34 | 1.75 | −5.92 | <0.001 |
| | 0.74 (conditional) | Days since release | 1, 4184 | −0.64 | 0.07 | −8.96 | <0.001 |
| | | Origin/age | 1, 4184 | 4.88 | 1.47 | 3.32 | 0.001 |
| | | Residential status | 1, 4184 | −2.96 | 1.10 | 2.68 | 0.007 |
| | | Season | 1, 4184 | 0.64 | 0.14 | 4.59 | <0.001 |
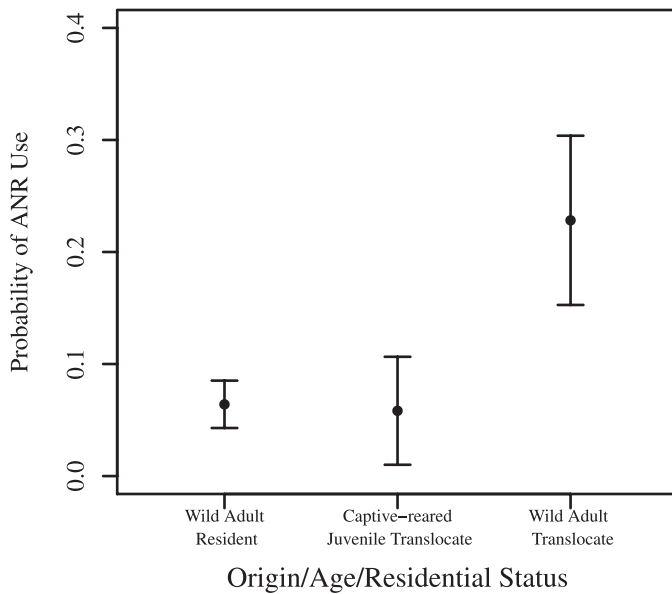
F<small>IG.</small> 4.—Mean probability (±1 SE) of artificial nest rock (ANR) use for wild resident adult, captive-reared translocated juvenile, and wild translocated adult Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) at two sites in the Blue River in Indiana.

(Gill 1979). Another factor that might explain the high site fidelity in our study was the use of soft-release cages. Boerner (2014) questioned the usefulness of soft releases; however, they are the most documented factor for increasing release site fidelity (Le Gouar et al. 2012). As such, we recommend their use during future Hellbender translocations. Future research should also focus on the effects of release cohort size and soft release techniques on site fidelity among Hellbenders.

Captive-reared juvenile translocates had lower site fidelity than wild adults in our study. All captive-reared juvenile translocates dispersed downstream with only one individual ever moving upstream from its release site (Fig. 1B). Although a greater number of downstream dispersals is typical in captive-reared juveniles (e.g., Boerner 2014), our subjects displayed lower site fidelity and higher mean dispersal distances than captive-reared juveniles in Missouri (Bodinof et al. 2012a). This was likely unrelated to their mean mass at release, because that value (218 ± 3 g) was greater than the cohort released in Missouri (202 ± 9 g; Bodinof et al. 2012b). One potential explanation for the decreased site fidelity and higher dispersal distances in our study is the timing of release. The Missouri study found that the season of release appears to affect postrelease movement patterns (Bodinof et al. 2012a). The release date in autumn could have put the cohort at a disadvantage compared to one in summer that would have maximized the period of time that individuals were at release sites prior to regular high flow events. Furthermore, captive-reared juveniles were likely unprepared for conditions at the sites because they were only exposed to stationary water during their time in captivity (Reading et al. 2013; Kenison and Williams 2018). In the future, environmental enrichment should be explored to help condition captive-reared Hellbenders for life in a lotic system. Additional time in captivity to allow individuals to reach a larger size might also improve outcomes, and

exploring the optimal head-starting period to maximize survival while minimizing cost is an important research avenue.

Although movement probabilities were comparable to those reported previously (Ball 2001; Bodinof et al. 2012a), mean movement distances in our subjects were greater than those previously reported (Hillis and Bellis 1971; Humphries and Pauley 2005). Even when movements greater than 500 m were excluded from home range calculations, the mean home range size for our subjects was 6–40 times greater than values reported previously (Blais 1996; Peterson and Wilkinson 1996; Humphries and Pauley 2005). Although some of this discrepancy arose from methodological considerations including the use of radio telemetry data and the large number of locations per individual (Obbard and Brooks 1981), ours is not the first study to suggest that Hellbenders in Indiana have larger home range sizes than individuals in the rest of the range (Burgmeier et al. 2011a). These increased home ranges might be attributable to unique Hellbender population demography or habitat composition in Indiana streams (Burgmeier et al. 2011b,c).

Another unusual movement pattern in our study was the prolonged exploratory period. Movement probabilities and monthly home range sizes both decreased with increasing time since release. Both residents and translocates settled into sites gradually, with even resident home ranges failing to stabilize fully until the second summer of the study (Fig. 3). This result was unexpected, because previous studies reported that translocates settle into permanent home ranges within 90 d (Gates et al. 1985; Bodinof et al. 2012a; Boerner 2014). The seasonal effects on movement patterns further complicated these results. During autumn, we saw higher movement probabilities, greater movement distances, and larger LHR sizes than in summer (Fig. 3). This increase in movement corresponds with the breeding season and has been demonstrated in other movement studies (Blais 1996; Burgmeier et al. 2011a). The strength of the effect in our study was unexpected, however, with mean monthly LHRs more than doubling during autumn compared to summer (Fig. 3). Because of these strong temporal signals, we suggest that long-term monitoring could be required to understand fully the effects of translocations on Hellbender movement patterns.

The group-level differences in movement patterns were largely driven by residential status as opposed to management or origin/age. Movement probability was the only movement model in which management or origin had an effect. The decreased movement probabilities at managed sites compared to unmanaged sites, combined with the relative stability of movement distances and home range size in residents, indicates they were minimally disrupted by the addition of translocates at sites. Translocates exhibited movement differences compared to residents, maintaining greater movement distances and larger home range sizes throughout the entire study period (Fig. 3). Although a pattern of increased movement in translocates compared to residents is common among herpetofauna (Rittenhouse et al. 2007; Nussear et al. 2012), it is often accompanied by a corresponding decrease in survival (Reinert and Rupert 1999; Hester et al. 2008). We saw no corresponding survival differences between wild translocates and residents (Kraus et al. 2017), and this was likely because of the observed

patterns of habitat use. Captive-reared translocates had a small but significant decrease in movement probability compared to wild adults, which might be explained by the fact that, at 5 yr old, they were sexually immature. Hellbenders might not reach sexual maturity until 6 yr, and our male subjects did not show the characteristic swollen cloaca during the breeding season (Petranka 1998). Adult movement probabilities peaked during the fall breeding season, and we would not expect a corresponding increase in immature juveniles.

Habitat use was similar at managed and unmanaged sites and between wild adult residents and translocates. Mean shelter rock size was comparable to, and the mean number of surrounding shelter rocks was slightly higher than, previous reports for this population (Burgmeier et al. 2011b). Both shelter rock size and number of surrounding shelter rocks were comparable between wild translocates and residents. These results are encouraging because they indicate that the habitat at the release sites was adequate and neither residents nor wild translocates experienced displacement to inferior habitat. Another promising result is that wild adult translocates had a higher probability of ANR use than other cohorts (Fig. 4C). Wild adult translocates appear to have benefited most from the presence of ANRs. We suggest that the frequent use of ANRs by our subjects early in the study, during the period when translocates were most vulnerable to mortality from predation and stress (Teixeira et al. 2007), might have facilitated their transition into the release site. Supportive measures, such as habitat supplementation, have been shown to increase translocation success in other taxa (Fischer and Lindenmayer 2000), but this is the first study to demonstrate the potential of habitat supplementation at translocation sites for Hellbenders.

Although captive-reared juvenile translocates demonstrated few movement differences from wild adult translocates, they differed greatly in their habitat use. Captive-reared juveniles used shelter rocks that were, on average, nearly half the size of those used by wild adults (Fig. 4A). This age-associated difference in shelter rock size has been noted previously (Nickerson et al. 2003). Captive-reared juveniles also used habitats with less surrounding cover than adults (Fig. 4B), however, indicating they utilized inferior habitat compared to wild adults. It is unclear whether this decrease in habitat quality was the result of direct competition with adults or occurred because subjects were swept out of high-quality habitat located in the release site. Unlike wild adult translocates, captive-reared juveniles rarely made use of the ANRs (Fig. 4C). Other studies have also suggested that ANRs are not often used in either wild (Jachowski 2016) or captive-reared (Boerner 2014) juveniles. These differences in habitat use were accompanied by reduced survival in the captive-reared juvenile cohort (Kraus et al. 2017). Because captive-reared juveniles will undoubtedly be important for future Hellbender conservation efforts, we advocate exploring techniques to improve translocation success in this life-history stage. In particular, habitat supplementation that specifically targets smaller age classes (e.g., cobble beds) could improve the success of captive-reared juveniles during future release efforts.

As with movement patterns, temporal factors were also significant in the habitat-use models, although the effect was not as strong. Hellbenders used shelter rocks with more

surrounding cover initially, which could be caused by an increased level of vigilance upon release in a new environment (Dickens et al. 2010). Hellbenders used both smaller and less sheltered boulders during the breeding season, reflecting a slight discrepancy between nesting and shelter habitat. Artificial nest rock use was also greater during the breeding season (autumn), an unsurprising trend given that ANRs were designed as nesting habitat (Briggler and Ackerson 2012) and increased ANR occupancy has been documented during the breeding season (Jachowski 2016). Breeding also likely explains the observed sex-related difference, with males using boulders with less surrounding cover than females. Because males must actively search for and attempt to attract mates (Nickerson and Mays 1973), this behavior could represent a trade-off between safety and increased breeding opportunities.

The results of this study indicate that site-level population augmentation might be an appropriate management technique to increase local densities and encourage breeding in low-density populations of Hellbenders. Augmentations appeared to have few negative effects on patterns of movement or habitat use in adult residents or wild adult translocates. Wild adult translocates fared much better than captive-reared juvenile translocates, which were more likely to leave release sites and utilize marginal habitat than their wild adult counterparts. We have also demonstrated the suitability of wild adult Hellbenders for augmentations at a local scale. Further evidence of success includes three nests discovered at Site 1 during the 4 yr following the augmentation efforts, allowing for the establishment of a captive-rearing program for Indiana Hellbenders (Williams and Kenison 2015). Potentially important factors in the success of this augmentation were adequate habitat availability at release sites and the use of support techniques, including soft releases and habitat supplementation.

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