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POSTRELEASE MOVEMENTS OF CAPTIVE-REARED OZARK HELLBENDERS (*CRYPTOBRANCHUS ALLEGANIENSIS BISHOPI*)

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ABSTRACT: Postrelease movements can determine the success of wildlife translocations. We monitored movements of 36 captive-reared Ozark Hellbenders (*Cryptobranchus alleganiensis bishopi*) released to augment wild populations at two sites on the North Fork of the White River (Missouri, USA). We used radiotelemetry to collect 3610 Hellbender locations from May 2008 to August 2009. We quantified movements at multiple spatio-temporal scales and made comparisons between two seasons of monitoring (1 5 release–December 2008; 2 5 January 2009–August 2009). At the finest (daily) scale, most Hellbenders (90%–94% per season) were highly sedentary (50% of observations indicated no movement). Typical distances between daily locations when Hellbenders moved were ≈ 5 m in Season 1 (median ≤ 3.08 m, $n = 331$; range ≤ 0.19 –903.00) and ≈ 2 m in Season 2 (median ≤ 1.80 m; $n = 161$; range ≤ 0.21 –34.00). During the study Hellbenders rarely (35 of 492 movements) travelled ≥ 20 m between daily locations, and virtually all (34 of 35) such movements occurred in Season 1. At a broader scale, home ranges of Hellbenders varied widely in Season 1 (range 5.066 –986.92 m², $n = 26$), but in Season 2 averaged only 31.33 m² (6 11.81 SE, $n = 58$) and 11.08 m² (6 3.25 SE, $n = 7$) at respective sites. Among Hellbenders monitored long enough to exhibit settlement (estimation of a home range) 69% (18 of 26) dispersed ≥ 50 m from the point of release. We only noted mortality associated with dispersals ≥ 50 m at one site, when it coincided with abandonment of core habitat that was one-third as large as at the other site. At the broadest scale, 68% and 86% of Hellbenders settled in core habitat of respective release sites, and most had settled within 21 d postrelease (range 5 0–49 d). Collectively, Hellbender movements indicated a short period of exploration followed by more permanent settlement and high site fidelity typical of wild conspecifics. Captive-reared juvenile Hellbenders may be well suited for translocation; however, the quality of habitat at fine scale (10–30 m²) and the extent of suitable habitat within release sites are important considerations.

Key words: Amphibian; Captive-reared; *Cryptobranchus alleganiensis*; Hellbender; Home range; Movement; Release site fidelity; Translocation

ANIMAL MOVEMENTS can determine the success of reintroduction and translocation programs (Fischer and Lindenmayer, 2000; Armstrong and Seddon, 2008; Germano and Bishop, 2009). In response to global amphibian declines (Houlahan et al., 2000; Stuart et al., 2004), captive rearing and translocation are increasingly used to augment or replace populations of declining or extirpated frogs and salamanders (Gascon et al., 2007; Bowkett, 2009). Amphibian translocations have been viewed as largely unsuccessful in the past (Dodd and Seigel, 1991). In a recent review, only 50% of 38 amphibian translocation

programs achieved success (Germano and Bishop, 2009). Among failed translocations examined by Germano and Bishop (2009), homing and long-distance movements away from release sites were the most commonly cited causes for translocation failure. For translocated wild adult amphibians homing behavior can result in swift abandonment of release sites (Matthews, 2003; Huste et al., 2006). In contrast, translocation of eggs or juvenile amphibians may lead to increased site fidelity and therefore successful establishment of a population (Cooke and Oldham, 1995; Semlitsch, 2002). Amphibian translocation success may also be positively associated with the release of large numbers of individuals (i.e., ≥ 1000 ; Germano and Bishop, 2009). However, captive-rearing such large numbers of amphibians can be costly, especially for relatively large,

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fully aquatic species. Pilot translocation programs involving relatively few, closely monitored individuals may be particularly useful for identifying factors affecting release site fidelity prior to rearing and releasing large numbers of individuals.

Translocation of captive-reared individuals is one strategy being considered to augment rapidly declining Hellbender (*Cryptobranchus alleganiensis*) salamander populations throughout the species' range. Hellbenders are large (up to 74 cm), fully aquatic, long-lived (25+ yr) amphibians (Taber et al., 1975) that require clean, flowing, highly oxygenated water, with prevalent rocky substrate. Two subspecies of Hellbender have been described, including the Eastern Hellbender (*C. a. alleganiensis*), which occurs from New York, USA, south to Georgia, USA, and west into Missouri, and the Ozark Hellbender (*C. a. bishopi*), which is endemic to the Black and White river drainages of southern Missouri and northern Arkansas, USA. Both subspecies have experienced declines (Furniss et al., 2003; Mayasich et al., 2003; Foster et al., 2009). Quantitative evidence has confirmed declines averaging 77% for both subspecies in Missouri alone (Wheeler et al., 2003). Proximate causes for Hellbender declines may include decreased water quality (Huang et al., 2010), overharvesting (Nickerson and Briggler, 2007), introduced predators (Gall and Mathis, 2010), and disease (e.g., chytridiomycosis; Briggler et al., 2008). Translocation of captive-reared Hellbenders may be useful for augmenting wild populations until the drivers of decline can be pinpointed, especially where suitable physical habitat still occurs.

A major concern of translocating Hellbenders is whether individuals will settle in release sites with suitable habitat and remnant populations. Hellbenders are habitat specialists that feed almost entirely on crayfish (Bishop, 1941; Nickerson and Mays, 1973a,b) and are typically associated with the occurrence of boulder substrate, which they use for shelter and breeding. In many streams, suitable Hellbender habitat (i.e., large patches of boulder) is nonrandomly distributed but occurs in discrete patches separated by long (~100 m) expanses of bedrock or fine substrate where protective cover is lacking (Nickerson and Mays, 1973b).

Wild Hellbenders naturally exhibit high site fidelity (Nickerson and Mays, 1973a) and small home ranges (Peterson and Wilkinson, 1996). However, following translocation wild Hellbenders exhibit homing (Hillis and Bellis, 1971; Blais, 1989) and relatively long-distance (~1000 m) dispersal prior to settling (Gates et al., 1985). Due to the spatially discrete nature of potential release sites, long-distance movements may result in increased risk of mortality for translocated Hellbenders. Strong associations with native resources that lead to homing behavior may be lacking or reduced in captive-reared amphibians (Germano and Bishop, 2009). Therefore, captive-reared Hellbenders may exhibit higher release site fidelity and thus may be more suitable translocation subjects for augmenting extant populations at a discrete site.

As a first step in evaluating the efficacy of captive rearing and translocation as a conservation strategy for Ozark Hellbenders, we used radiotelemetry to monitor movements of 36 captive-reared juveniles that were released at two locations in the North Fork of the White River (hereafter NFWR), Missouri, for over 1 yr. We examined Hellbender movements at multiple spatio-temporal scales, using seven unique parameters to quantify movements (see Table 1 for definitions). We examined three hypotheses predicting post-release movement pattern. First, we tested the hypothesis that a lack of prior knowledge of release sites would result in exploratory movement, characterized by a higher proportion of daily observations indicating movement, longer distances between daily locations when Hellbenders moved, and larger home ranges in the first season of monitoring relative to the second. Second, we tested the hypothesis that translocated Hellbenders would initially settle in the wild within 90 d postrelease, similar to wild Hellbenders that were translocated to a new stream (Gates et al., 1985). Third, we tested the hypothesis that captive-reared Hellbenders would exhibit release site fidelity to "core habitat" (defined below) due to the strong association the species exhibits with large cobble and boulder substrate (Nickerson and Mays, 1973a,b) and because leaving core habitat in our study sites would require extensive travel away from boulders over exposed gravel-ripple beds.

TABLE 1.—Parameters used to quantify movement of captive-reared Ozark Hellbenders (*Cryptobranchus alleganiensis bishopi*) translocated to the North Fork of the White River, Missouri, 2008–2009.

Parameter	Spatial/temporal scale	Definition
Sedentariness	Fine/daily	Proportion of 0-m values (i.e., no movement) for the distance between pairs of sequential locations collected 24–36 h apart
Step length	Fine/daily	Distance (m) between pairs of sequential observations collected 24–36 h apart when hellbenders moved (i.e., $\neq 0$ m)
Home range	Meso/seasonal	A defined area (m ²) with a 50% (core home range) or 95% probability of occurrence of a hellbender during a given season
Dispersal distance	Meso/seasonal	The Euclidean distance between the point of release and the center of a hellbender Season 1 core home range
Dispersal window	Meso/seasonal	The number of days between release and the first observation of a hellbenders within its Season 1 core home range
Shift in activity center	Broad/multi-seasonal	The Euclidean distance between seasonal core home range centers
Release site fidelity	Broad/multi-seasonal	The number of hellbenders monitored for \$ the maximum dispersal window observed whose last observation in the study occurred in core habitat of release sites, divided by the number of hellbenders monitored for \$ the maximum dispersal window observed + the number of hellbenders monitored for any length of time whose last observation occurred outside of core habitat

MATERIALS AND METHODS

Study Sites

Our study occurred at two sites within the NFWR, which is a primarily spring-fed seventh-order stream that originates in Wright County, Missouri, before flowing south into Norfolk Reservoir. We selected translocation sites in the NFWR because captive-reared Hellbenders intended for release were hatched from eggs collected there in 2002 by Unger (2003). We restricted translocation of Hellbenders to their river of origin based on the apparent genetic isolation of Hellbender populations by drainage (Routman et al., 1994) and guidelines for animal reintroduction (IUCN, 1998). Though NFWR Hellbender populations have declined 70% since the mid-1980s (Wheeler et al., 2003), the river still supports a relatively large proportion of the extant Ozark Hellbender population and may represent the highest quality habitat remaining within the subspecies' range (Federal Register, 2010). Historic Hellbender densities from the NFWR are among the highest reported for the species in the literature, reaching an estimated one Hellbender per 8–10 m² and 428 Hellbenders per 1 km of stream bed in the early 1970s (Nickerson and Mays, 1973a). The abundance of crayfish and rock shelters apparently contributed to the high Hellbenders densities reported from the NFWR (Nickerson and Mays, 1973b). Three native crayfish species

occur in the NFWR, including *Orconectes neglectus*, *O. longidigitus*, and *O. punctimanus*. Beds of large dolomite and limestone slabs and deeply creviced bedrock remain prevalent, but are often separated by expansive pebble and gravel beds. Generally, current NFWR habitat appears extremely similar to descriptions from the 1970s (Nickerson and Mays, 1973b).

The two release sites (hereafter upper and lower) were separated by approximately 17 km of river. We do not reveal precise release site localities due to threats of illegal collecting and the current status of Hellbenders in Missouri. We selected sites that contained numerous large cobbles and boulders (Wentworth, 1922), some bedrock, and a variety of pools, runs, and riffles. Random sampling of runs and riffles (≈ 1 m deep), using a 1-m kick-seine technique (Mather and Stein, 1993) in August 2008, indicated that crayfish densities at the upper (12.16 crayfish/m² \pm 2.40 SE) and lower site (12.61 crayfish/m² \pm 1.52 SE) were similar. Between 2005 and 2007, thorough surveys of the upper ($n = 4$ surveys) and lower site ($n = 3$ surveys) yielded six and seven individual Hellbenders, respectively. Therefore, density of wild residents was assumed to be far below carrying capacity based on historical densities reported from river (Nickerson and Mays, 1973a).

We defined core habitat as the largest and most continuous patch of boulder within each site. At both sites, core habitat was bordered

by gravel–pebble beds that extended 300 m both up- and downstream. Core habitat in both sites appeared suitable for Hellbenders. However, we wanted to quantify site differences in factors that may influence Hellbender movements, such as the extent and arrangement of boulders during our study. To describe differences in the arrangement of boulders, we measured the shortest Euclidean distance to protective cover (i.e., substrate with an axis 30 cm long) as one aspect of boulder density, from random locations within core habitat at each site. To quantify the extent of core habitat (m^2) at each site, we generated digital maps of substrate from transect surveys. To generate maps, we estimated percentage of cover for unique substrate classes (as per Wentworth, 1922) within successive 1- m^2 quadrats along georeferenced cross-sectional transects of the river during August–September 2008. Transects were spaced approximately 5 m apart and, at each site, spanned 100 m upstream to 100 m downstream of the farthest up- and downstream surviving Hellbender location in August 2008. Digital substrate maps were interpolated using the natural neighbor function (1-m resolution) in the ArcGIS Spatial Analyst Toolbox. We quantified extent (m^2) of boulder within core habitat by summing the number of pixels with values of boulder ≥ 0.10 that occurred within polygons encompassing the reach of stream where core habitat occurred.

Study Animals

Between 2003 and 2008 we reared 36 Ozark Hellbenders hatched from a NFWR clutch collected in 2002 by Unger (2003). We reared Hellbenders in aquaria lined with flat rocks arranged over pebbles at the Saint Louis Zoo's Ron Goellner Center for Hellbender Conservation. We continuously aerated aquaria water and maintained temperatures to mimic southern Missouri streams. We tong-fed Hellbenders a diet of crayfish, Lake Smelt (*Osmerus* sp.), night crawlers, and krill. We weaned Hellbenders from tong-feeding approximately 6 mo prior to release; after which they demonstrated successful foraging in prey-stocked enclosures. We individually marked each Hellbender by injecting it with an AVID

passive integrated transponder. We confirmed absence of the chytrid fungus, *Batrachochytrium dendrobatidis*, in the release cohort via polymerase chain reaction assay of three swabs collected (as per Briggler et al., 2008) at weekly intervals just prior to release.

Prior to translocation, we surgically implanted nine Hellbenders with Sirtrack Limited model RVI 118 (30.3 × 13.3 × 8 mm, 5–6 g, 7.5-mo battery) and 27 Hellbenders with model RVI 218 (35.3 × 15.3 × 15 mm, 9–10 g, 15-mo battery) very high frequency radio transmitters. We only implanted Hellbenders if the unit weighed $\leq 5\%$ of Hellbender mass. Though model RVI 118 was not expected to last the duration of the study, for some Hellbenders this was the largest unit that met our required unit mass/body mass ratio. To allow time for smaller Hellbenders to reach weight sufficient for implant (140 g for RVI118 and 180 g for RV218), we staggered surgeries, which occurred at the Saint Louis Zoo on 3–4 May ($n = 20$), 7 July ($n = 7$), and 3 September ($n = 9$) 2008. At surgery, mean mass of Hellbenders was 202 g \pm 6.9 SE (range 5.142–334 g), mean total length was 319 mm \pm 6.4 SE (range 5.285–368 mm), and gender was unknown. We anesthetized Hellbenders individually by placing them in a 250 mg/L solution of tricaine methanesulfonate buffered with sodium bicarbonate (baking soda) added to saturation. We removed Hellbenders from the solution once they were immobile and their righting reflex was lost. We swabbed a 2- cm^2 area of the ventral body wall with dilute chlorhexidine solution before making a 2-cm incision opening to the body cavity, left of midline. We rinsed transmitters that had been cold-sterilized in Nolvasan for 24 h with sterile saline and placed them into the coelom. We closed the body wall muscle layers with three sutures and closed the skin with three (3/0 polydioxane or nylon) sutures. Finally, we injected each Hellbender with 10 mg/kg of enrofloxacin (antibiotic) and returned them to holding water where they were monitored until voluntary swimming occurred (within 30 min). We maintained Hellbenders in captivity for 2–4 wk prior to release unless dehiscing sutures were observed, in which case we repaired sutures and held Hellbenders until the next cohort was released.

Release and Monitoring

Following the staggered fashion of surgeries, we released Hellbenders in three seasonal cohorts during 2008. Release cohorts were identified as spring (May; $n = 5$, 17), summer (August; $n = 5$, 10), or autumn (October; $n = 5$, 9). Each cohort was randomly divided between release sites, for a total of 18 Hellbenders released at each site. We released Hellbenders by hand within core habitat at preselected rocks with a mean maximum diameter of 77 cm \pm 4 SE (range 52–161 cm). Release rocks were spaced 5 m from the nearest known Hellbender. We allowed Hellbenders to move under cover and recorded Universal Transverse Mercator coordinates of Hellbender locations with a Trimble GeoXT (Trimble Navigation Ltd., Sunnyvale, California, USA) handheld unit accurate to \pm 1.5 m.

We relocated Hellbenders by homing (White and Garrott, 1990) using a three-element Yagi antenna and an ATS receiver (model R2000, R4000 or R410, Advanced Telemetry Systems, Isanti, Minnesota, USA). We waded or canoed to locations while minimizing disturbance to habitat and animals, and confirmed ambiguous locations visually by snorkeling or with an Aqua-Vu SV 100 camera (Outdoor Insights, Crosslake, Minnesota, USA). We relocated each Hellbender approximately every 24–36 h from release through 14 November 2008 and from 26 March through 21 August 2009. Between 15 November 2008 and 25 March 2009 we located Hellbenders approximately once each week.

Due to an interest in monitoring body condition of the experimental population as part of another study, we recaptured 19 Hellbenders just prior to their first winter (October–December 2008) and 12 Hellbenders in early spring 2009. We made an effort to minimize habitat disturbance and handling time during recaptures. We released recaptured Hellbenders at the site of capture within 30 min, with the exception of seven Hellbenders that were removed in early August 2008 ($n = 5$) or March–April 2009 ($n = 6$), transported to the Saint Louis Zoo for transmitter replacement surgery, and rereleased in May 2009 (8 wk–9 mo later).

Movement Data Analysis

We defined seasons of interest based on biologically relevant activity periods for Hellbenders. Hellbenders typically become highly sedentary during winter, but are more active during the remainder of the year (Ball, 2001). Our first season of monitoring (hereafter referred to as Season 1; release–31 December 2008) encompassed the active period leading into winter dormancy, and our second season (Season 2; 1 January–19 August 2009) encompassed the active period following winter dormancy.

Daily movements.—As a metric to describe Hellbender movements at a fine (i.e., daily) spatio-temporal scale, we first calculated the straight-line distance (m) between each pair of sequential locations collected 24–36 h apart, using the “calculate movement parameters” function in the Hawth’s Tools Extension (Beyer, 2004). For each site, we calculated sedentariness (Table 1), as the proportion of 0-m distances observed for each Hellbender with ≥ 20 observations in a given season. We were interested in the distance between sequential locations when Hellbenders moved, regardless of how long they were monitored over the course of the study. Therefore, we summarized step lengths (Table 1) at the individual and population level, after removing 0-m distances.

Home range.—To describe Hellbender movements over a meso (i.e., seasonal) spatio-temporal scale, we calculated the size of individual Hellbender home ranges (Table 1) within Season 1 and Season 2, separately. To avoid potential positive bias in home range size due to spurious movements that occurred shortly after translocation we first removed all locations collected ≤ 14 d post-release and calculated home range size for each Hellbender with ≥ 20 locations remaining in a given season. We calculated 50% (i.e., core home ranges) and 95% fixed kernel (FK) utilization distributions using the plug-in method for bandwidth selection and the package “ks” (Duong, 2008) in program R (R Development Core Team, 2006). Similar to many herpetofauna, Hellbenders tend to remain in the same location, which can cause problems with kernel estimation of utilization distributions (Row and Blouin-Demers, 2006). Following the approach of Getz and Wilmer

(2004) and Getz et al. (2007), we randomly distributed duplicate locations (Skalski, 1987) within a radius of 40 cm (approximately one-half the mean length of rocks used by Hellbenders in our study) before calculating utilization distributions. We applied kernel methods as opposed to more commonly used (i.e., minimum convex polygon [MCP]) home range estimators because kernel methods account for variation in intensity of use throughout a home range, and because MCP estimates are highly sensitive to sampling intensity and time scale of a study, thereby limiting the potential for comparison of our results with future studies (Bo" rger et al., 2006).

To account for variation in the length of time Hellbenders were monitored during Season 1 due to the staggered release, we report mean home range size during Season 1 separately for each release cohort but pooled cohorts to estimate mean home range size in Season 2. Because recapture and removal of Hellbenders for transmitter replacement surgeries in spring 2009 may have influenced Hellbender movements, we did not include home ranges of animals that were removed for transmitter replacement in our estimates of mean home range size during Season 2.

Dispersal distance and window.—We calculated dispersal distances (Table 1) within

Season 1 separately for each Hellbender whose Season 1 home range could be estimated. To calculate the center of polygons representing core home ranges we use the "feature to point" tool in ArcGIS. When the straight-line path between release locations and core home range centers crossed outside of the river corridor (e.g., because of a bend in the river) we calculated dispersal distance as the shortest path within the river channel between release and core home range center.

We quantified dispersal window (Table 1) as the time between release and the first location within the Season 1 core home range polygon, which we assessed by overlaying

Hellbender locations on these polygons in ArcGIS. We report dispersal distance separately for each Hellbender, and report mean dispersal window separately for each cohort.

Shift in activity center and release site fidelity.—Because our definition of dispersal

was based on a relatively short period of monitoring (i.e., #8 mo), we estimated the mean shift in activity center (Table 1) between Seasons 1 and 2 as a broad spatio-temporal measure of Hellbender site fidelity to the general area where they initially settled. We calculated shift in activity center separately for each Hellbender whose home range could be estimated in both seasons using points representing core home range centers and the "point distance" tool in ArcGIS. We report mean shift in activity center (m) after pooling release cohorts.

As another broad spatio-temporal measure of Hellbender movement, we calculated release site fidelity (Table 1) separately for each site. All mean values are reported ± 1 SE.

RESULTS

We collected 3610 Hellbender locations (mean ± 100 locations/hellbender ± 12 SE locations/Hellbender; range 5–213) from 19 May 2008–19 August 2009. We confirmed 13 mortalities over the course of our study. Five mortalities occurred within 30 d postrelease, three within 50 to 92 d postrelease, and five within 126 to 369 d postrelease. Twenty-two Hellbenders were confirmed alive and continued to be monitored in May 2009, approximately 3 mo before the end of our study. Bodinof et al. (in press) provides a more thorough assessment of Hellbender survivorship during our study.

We noted distinct site differences in the arrangement and extent of boulders within core habitat. Although core habitat was distributed along an approximate 350-m reach at both sites, boulder covered a three-fold greater extent in lower site core habitat (6470 m²) than in upper site core habitat (2363 m²). In addition to covering a smaller extent, boulders were more patchily arranged at the upper site, where the mean distance from boulder-cobble to "protective cover" (0.59 m ± 0.26 SE; $n = 5$; range 0–25 m) was almost two-fold greater than within the lower site (0.34 m ± 0.10 SE; $n = 5$; range 0–32 m).

Daily Movements

We found support for our hypothesis that lack of knowledge of release sites would result

in a larger proportion of daily observations indicating movement (i.e., lower sedentariness) and larger step lengths during the first season of monitoring. Most Hellbenders (90%–94% per season; Tables 2 and 3) exhibited relatively high sedentariness (e.g., $\bar{x} = 0.50$) during the study, regardless of season. However, 11 of 13 Hellbenders monitored for both seasons maintained or increased sedentariness during Season 2, when about 80% of daily observations per Hellbender indicated no movement at both sites (upper: mean $\bar{x} = 0.83 \pm 0.04$ SE; lower: $\bar{x} = 0.80 \pm 0.04$ SE; Tables 2 and 3).

In addition to becoming more sedentary, Hellbenders were less likely to exhibit long-distance step lengths during Season 2. Collectively, we observed 331 nonzero daily step lengths during Season 1 ($n = 34$ of 36 Hellbenders monitored; mean $\bar{x} = 9.74$ step lengths/Hellbender ± 1.97 SE) and 161 step

lengths during Season 2 ($n = 18$ of 25 Hellbenders monitored; mean $\bar{x} = 8.94$ step lengths/Hellbender ± 1.40 SE; Tables 2 and 3). During both seasons, most step lengths were 1–5 m, and few (35 of 492 step lengths) exceeded 20 m (Fig. 1A, B). However, the site-specific distribution of step lengths in Season 1 indicated that Hellbenders at the upper site, where boulders were more patchily arranged, tended to travel longer distances on a daily basis. During Season 1, median step length was about one-third larger (upper: 3.59 m, $n = 113$, range $\bar{x} = 0.23$ –903.33 m; lower: 2.62 m, $n = 218$, range $\bar{x} = 0.19$ –468.87 m), and step lengths ≥ 20 m were about four times more common (upper: 20.35% of step lengths; lower: 5.05% of step lengths) at the site with patchily arranged boulders, despite the fact that about half the Hellbenders released at each site (upper: 10 of 18; lower: 7 of 18) exhibited at least one step length ≥ 20 m. During Season 2, median step

TABLE 2.—Parameters describing movements and home range size of juvenile captive-reared Ozark Hellbenders (*Cryptobranchus alleganiensis bishopi*) posttranslocation to the upper site in the North Fork of the White River, Missouri, during Season 1 (release–31 Dec 2008) and Season 2 (1 January 2009–19 August 2009). Numbers in parentheses indicate sample size and numbers within brackets represent the range of observed values.

ID	Season 1			Season 2		
	Sedentariness ^a	Step length ^b	Home range ^c	Sedentariness ^a	Step length ^b	Home range ^c
Spring cohort						
110	0.76	10.22 (9) [0.35–114.82]	19.41	* ^d	*	*
180	— ^e	48.17 (6) [12.00–783.52]	—	*	*	*
190	0.89	3.54 (7) [0.75–9.80]	15.85	1.00	(0)	3.26
210	0.91	1.29 (6) [0.30–13.00]	19.07	0.65	1.94 (16) [0.40–16.00]	27.01
240	0.72	1.65 (19) [0.32–5.00]	21.40	0.80	0.80 (11) [0.40–11.00]	12.80
250	0.60	10.90 (12) [1.01–36.20]	¥ ^f	—	—	—
260	0.92	43.21(5) [1.20–62.17]	315.88	0.96	1.45 (2) [1.00–1.90]	13.74
Summer cohort						
20	0.74	1.60 (7) [0.23–94.00]	22.52	*	*	*
160	0.81	4.94 (7) [0.40–28.50]	114.21	0.81	1.70 (10) [0.32–9.49]	19.98
230	0.52	8.22 (10) [1.70–482.97]	¥	*	*	*
1030	0.67	1.65 (12) [0.85–5.20]	22.30	0.78	2.41 (12) [0.69–8.20]	27.20
1090	—	11.00 (1)	—	*	*	*
1470	—	19.00 (3) [3.40–57.63]	—	*	*	*
Autumn cohort						
1130	—	452.49 (2) [1.65–903.34]	—	—	—	—
1630	—	1.52 (4) [0.70–6.01]	17.22	—	4.25 (1)	4.72 ^g
1650	—	1.64 (1)	3.17	—	—	—
1670	—	1.90 (1)	7.92	0.75	4.63 (6) [0.90–7.16]	36.79
1690	—	24.00 (1)	14.18	0.91	17.78 (2) [1.57–34.00]	109.88

^a Proportion of 0-m values for the distance between sequential daily observations collected 24–36 h apart.
^b Median non-zero distance (m) between sequential daily locations collected 24–36 h apart.
^c Estimated 95% fixed kernel home range size (m²; may include locations collected ≥ 36 h apart that may not be evident in step-length summary).
^d Asterisk (*) indicates that mortality or signal loss prevented monitoring during the given season.
^e — indicates that low sample size (< 20 observations) during the given season prevented an estimate.
^f ¥ indicates gross overestimate due to tight clustering of locations separated by long distances.
^g Estimate for an individual that was temporarily removed for transmitter replacement in the given season.

TABLE 3.—Parameters describing movements and home range size of juvenile captive-reared Ozark Hellbenders (*Cryptobranchus alleganiensis bishopi*) posttranslocation to the lower site in the North Fork of the White River, Missouri, during Season 1 (release–31 Dec 2008) and Season 2 (1 January 2009–19 August 2009). Numbers in parentheses indicate sample size and numbers within brackets represent the range of observed values.

ID	Season 1			Season 2		
	Sedentariness ^a	Step length ^b	Home range ^c	Sedentariness ^a	Step length ^b	Home range ^c
Spring cohort						
10	0.88	6.60 (9) [0.67–21.41]	40.88	0.95	1.96 (3) [1.68–2.35]	3.09
40	0.81	1.08 (12) [0.46–1.57]	22.14	0.87	0.80 (8) [0.21–12.00]	9.82
70	— ^d	29.38 (2) [16.64–42.11]	—	* ^e	*	*
90	1.00	(0)	0.66	—	(0)	—
100	0.51	3.15 (32) [0.34–30.50]	951.81	0.75	1.90 (15) [0.56–4.60]	19.07
120	0.28	2.56 (50) [0.35–65.31]	986.92	1.00	(0)	8.15
130	0.54	3.08 (31) [0.38–14.00]	408.07	*	*	*
150	—	12.58 (7) [4.94–18.20]	*	*	*	*
200	0.45	2.12 (37) [0.50–19.24]	457.60	0.65	1.94 (16) [0.52–17.00]	338.24 ^f
220	—	17.27 (4) [6.32–70.58]	*	*	*	*
Summer cohort						
1170	0.64	1.75 (11) [0.19–22.00]	75.80	0.73	2.20 (16) [0.70–4.58]	10.84
1250	0.58	1.27 (12) [0.40–5.31]	27.02	*	*	*
1430	—	4.98 (1)	—	*	*	*
1510	1.00	(0)	0.74	0.95	1.80 (3) [1.80–1.80]	1.11
Autumn cohort						
1230	—	4.55 (1)	5.60	—	9.26 (2) [5.35–13.18]	—
1050	—	1.58 (6) [0.62–9.00]	11.55	0.59	1.21 (19) [0.36–8.36]	15.55 ^f
1190	—	268.62 (2) [68.36–468.88]	1.09	0.79	1.49 (12) [1.00–8.30]	25.50
1710	—	3.21 (1)	11.32	0.73	4.53 (7) [1.65–13.85]	224.55 ^f

^a Proportion of 0-m values for the distance between sequential daily observations collected 24–36 h apart.

^b Median non-zero distance (m) between sequential daily locations collected 24–36 h apart.

^c Estimated 95% fixed kernel home range size (m²; may include locations collected < 36 h apart that may not be evident in step-length summary).

^d — indicates that low sample size (< 20 observations) during the given season prevented an estimate.

^e Asterisk (*) indicates that mortality or signal loss prevented monitoring during the given season.

^f Estimate for an individual that was temporarily removed for transmitter replacement in the given season.

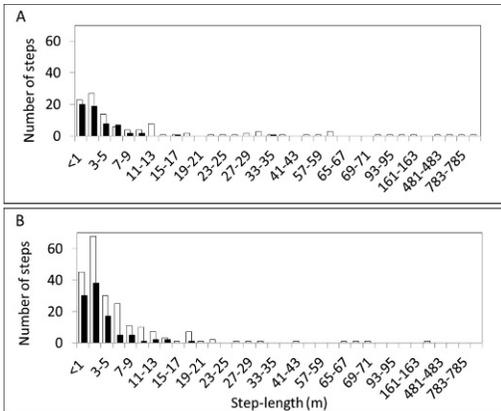


FIG. 1.—Distribution of daily (non-zero) step lengths at the upper (A) and lower (B) sites in the North Fork of the White River, Missouri, where captive-reared Ozark Hellbenders (*Cryptobranchus alleganiensis bishopi*) were translocated, 2008–2009. White bars represent step-length data from Season 1 and dark bars represent data from Season 2.

length was almost identical between sites (upper: 1.83 m, *n* = 60, range = 0.32–34.00 m; lower: 1.80 m, *n* = 101, range = 0.22–17.00 m), and step lengths > 20 m were virtually absent from both sites (upper: *n* = 5; lower: *n* = 0).

Home Range

We calculated 95% FK home ranges for 28 Hellbenders in Season 1 and 15 Hellbenders in Season 2. However, two home range estimates in Season 1 were grossly overestimated because they included broad areas between tight clusters of locations that were separated by over 50 m, and were discarded from further analysis.

We found partial support for our hypothesis that Hellbenders would use smaller home ranges during Season 2. At both sites, the length of time individuals were monitored due to a staggered release was positively associated with mean home range size in Season 1.

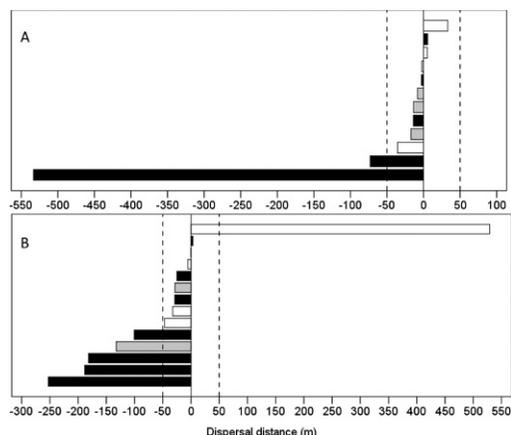


FIG. 2.—Direction and distance (m) of dispersal for 26 (upper site: $n = 12$; lower site: $n = 14$) captive-reared Ozark Hellbenders (*Cryptobranchus alleganiensis bishopi*) translocated to the upper (A) and lower (B) sites in the North Fork of the White River, Missouri, 2008–2009. Dispersal distances were calculated as the Euclidean distance between the point of release and the center of Season 1 home range centers, for individuals whose Season 1 home range could be estimated. Bars represent individuals released in spring (black bars), summer (gray bars), and autumn (white bars). Net direction of dispersal, relative to the point of release, is indicated by positive (upstream) and negative (downstream) values.

During Season 1, mean home range estimates were largest for the spring cohort (upper: $78.32 \text{ m}^2 \pm 659.93 \text{ SE}$; lower: $409.73 \text{ m}^2 \pm 6160.57 \text{ SE}$) followed by the summer cohort (upper: $53.01 \text{ m}^2 \pm 630.60 \text{ SE}$; lower: $34.52 \text{ m}^2 \pm 621.99 \text{ SE}$) and smallest for the autumn cohort (upper: $10.62 \text{ m}^2 \pm 63.15 \text{ SE}$; lower: $7.39 \text{ m}^2 \pm 62.51 \text{ SE}$; Tables 2 and 3). Among Hellbenders whose home range was estimated in both seasons, spring- and summer-released Hellbenders were more likely to decrease their home range size in Season 2 than autumn-released Hellbenders, who all increased their home range 3- to 22-fold (Tables 2 and 3). Despite the trend of autumn-released Hellbenders to increase home range size, all but one Hellbender had home ranges estimated to be $> 40 \text{ m}^2$ in Season 2 (Tables 2 and 3).

Dispersal Distance and Window

Eighteen of 26 (69%) Hellbenders whose home range was estimated during the first season dispersed less than 50 m from the point of release, and most (20 of 26) dispersed downstream (Fig. 2A,B). Upper-site Hellbenders

tended to settle extremely close to the point of release or about 500 m away (Fig. 2A) in the nearest patch of boulder downstream of core habitat. In contrast, one-third ($n = 6$) of the Hellbenders released at the lower site, where the extent of core habitat was about 1.5-fold larger, dispersed farther than 50 m (Fig. 2B). Five lower-site Hellbenders that dispersed farther than 50 m remained in core habitat and one Hellbender dispersed to the nearest patch of boulder (about 500 m) upstream of core habitat. The proportion of spring-cohort Hellbenders that dispersed farther than 50 m at the upper (40%) and lower (57%) sites was at least 1.7-fold larger than proportions of summer (upper site 5.0%; lower site 5.33%) or autumn cohorts (upper site 5.0%; lower site 5.25%) to disperse farther than 50 m at either site.

We found strong support for our hypothesis that Hellbenders would settle within 90 d postrelease. Most Hellbenders (20 of 26 or 76.9%) had entered their Season 1 core home range within 21 d postrelease, and the maximum dispersal window we observed was 49 d. Similar to the greater variation and longer dispersal distances noted at the lower site, the mean dispersal window for lower site Hellbenders released in spring ($19.85 \text{ d} \pm 66.24 \text{ SE}$, $n = 7$), summer ($16.66 \text{ d} \pm 614.46 \text{ SE}$, $n = 3$), and autumn ($10.25 \text{ d} \pm 62.84 \text{ SE}$, $n = 5$) was more variable and tended to be longer than for any cohort of upper site Hellbenders (spring 5.13.80 d $\pm 65.20 \text{ SE}$, $n = 5$; summer 5.10.00 d $\pm 69.53 \text{ SE}$, $n = 3$; autumn 5.8.75 d $\pm 63.15 \text{ SE}$, $n = 4$).

Shift in Activity Center and Release Site Fidelity

Over the course of our study, Hellbenders exhibited high site fidelity to the general area where they settled within a few weeks of release. Among Hellbenders monitored in both seasons, the average shift in activity centers was only $9.08 \text{ m} \pm 63.65 \text{ SE}$ ($n = 8$; range 5.0.35–32.34 m) at the upper site and only $13.01 \text{ m} \pm 66.28 \text{ SE}$ ($n = 7$; range 5.0.94–45.28 m) at the lower site.

We found support for our hypothesis that Hellbenders would remain within core habitat to avoid travelling long distances away from protective cover. Twenty-nine Hellbenders

were monitored for at least 49 d and two additional Hellbenders were monitored for shorter periods but were last observed outside of core habitat. Release site fidelity at the lower site (13 of 15 or 86%) was about 1.5-fold higher than at the upper site (11 of 16 or 68%). Though Hellbenders released in spring were more likely to disperse long distances (i.e., >50 m) than other cohorts, the proportion of spring-released Hellbenders that left core habitat was about three-fold larger at the upper site (three of seven) compared to the lower site (one of eight).

All seven Hellbenders confirmed to have left core habitat did so within 45 d postrelease. Among the five Hellbenders that left upper-site core habitat, three ultimately died and two were alive at the end of the study. Among lower-site Hellbenders that left core habitat, one was alive at the end of the study and the transmitter of the other continued to emit a signal but fate of the animal could not be confirmed.

DISCUSSION

Captive-reared Hellbenders proved capable of making long-distance movements over a short period of time, yet their tendency was to quickly settle within core habitat of release sites and establish small home ranges where they remained over the course of our study. The sedentariness and relatively high release site fidelity of Hellbenders in our study contrasts sharply with the high rates of movement and release site abandonment that have been described for several other species of herpetofauna following translocation (Reinert and Rupert, 1999; Matthews, 2003; Tuberville et al., 2005; Fellers et al. 2007). Our findings indicate that juvenile Hellbenders subject to captive rearing tend to exhibit movements compatible with goals to augment or reestablish populations where suitable habitat exists.

The extremely quick time to settlement (about 21 d) and high release site fidelity exhibited by Hellbenders in our study may have been attributable to life stage, conditions of captive rearing, or the quality of core habitat. Wild Hellbenders translocated to a new stream in Maryland, USA, dispersed an average of 1036 m \pm 289 SE (range 5

0–2340 m) before settling around one or more rocks, which typically occurred between 30 and 90 d postrelease (Gates et al., 1985). Given the homing tendencies and long dispersals exhibited by wild Hellbenders, our findings indicate that wild adults may be less suitable translocation subjects than captive-reared juveniles. Translocation of immature Gopher Tortoises (*Gopherus polyphemus*; Tuberville et al., 2005) and eggs, captive-reared larvae, or juveniles of several pond-breeding amphibians (Cooke and Oldham, 1995; Kinne, 2004) have resulted in increased site fidelity relative to translocation of mature herpetofauna (e.g., Cooke and Oldham, 1995; Matthews, 2003; Huste et al., 2006). One explanation for increased release site fidelity in captive-reared or immature animals may be lack of a habitat template (e.g., Rittenhouse et al., 2007) or reduced fidelity to specific resources (e.g., dens or ponds) from past environments (Semlitsch, 2002; Germano and Bishop, 2009). Because attempts to seek out familiar resources can result in “homing” to original capture sites (Stamps and Swaisgood, 2007:393), rearing Hellbenders in conditions similar to the wild may have increased the probability that they would identify release sites as suitable (e.g., Wiens, 1970, 1972). Physical habitat throughout both study sites appeared consistent with descriptions of habitat where high densities of Hellbenders were found in the 1970s (Nickerson and Mays, 1973a,b). Therefore, core habitat at release sites may have fit an innate habitat template (e.g., Wiens, 1970, 1972) for captive-reared Hellbenders or been of higher quality than habitat where wild Hellbenders have been translocated (e.g., Gates et al., 1985). One factor that may have influenced site fidelity that we did not examine is the density of wild conspecifics, especially since Hellbenders are considered territorial and sometimes show aggressive defense of rock shelters (Smith, 1907). Although our study confirms that captive-reared Hellbenders can show high site fidelity to release sites, more research is needed to identify factors that motivate long-distance movements in Hellbenders.

Available evidence indicates that captive-reared Hellbenders began moving similar to

wild Hellbenders by the end of our study. Our research is the first to intensively monitor ~20 Hellbenders using methods other than lifting rocks to locate animals. Therefore it is difficult to compare our results with others. However, the mean proportion of sequential observations showing no movement (0.89 ± 0.01 SE) for 10 wild Hellbenders radio-tracked for 15 mo in North Carolina USA (Ball, 2001), were similar to levels of sedentariness we observed in Season 2. Mean step length observed by Ball (2001; 14.67 m for females and 10.14 m for males) was five to seven times greater than median step lengths exhibited by translocated Hellbenders during Season 2, which may be due to variation in arrangement of boulders, location error, or variation in sampling strategy. Over a broader temporal scale, captive-reared Hellbenders in our study used extremely small home ranges following winter, similar to the size of home ranges and activity areas reported for wild Hellbenders in the NFWR (Nickerson and Mays, 1973a,b), Niangua River (Missouri; Peterson and Wilkinson, 1996), New York (Blais, 1989), and Pennsylvania, USA (Hillis and Bellis, 1971). We speculate that Hellbenders used larger home ranges in Season 1 primarily due to exploration prior to settlement. However, Season 1 included September and October, when mature Hellbenders are known to increase movement prior to breeding in the NFWR, which may also partially explain the seasonal difference in home range size. Only two of the 19 Hellbenders recaptured in late fall 2008 showed definite external signs of sexual maturity. However, some long-distance daily movements in Season 1 may have resulted from displacement of translocated individuals by mature wild residents migrating to nesting sites in weeks prior to breeding, or direct attempts by translocated animals to breed (See Bodinof et al., in press). Regardless of factors that may influence seasonal fluctuation in home range size, the minimal shift in seasonal activity centers and small home ranges evident in Season 2 indicate that fine-scale attributes (within 10–30 m²) are likely an important determinant of habitat suitability for Hellbenders, and should be considered when selecting future translocation sites.

The population level differences that we noted in movements at multiple spatio-temporal scales may be attributable to site differences in core habitat quality or quantity. At a fine scale, the increased proportion of step lengths exceeding 20 m in Season 1 at the upper site, where boulders arrangement was patchier, suggests daily step lengths during the exploratory phase may have been related to spacing between or availability of protective shelter sites. Bodinof et al. (2012) describe similarities in population level resource selection patterns exhibited by Hellbenders in the current study. Resource selection patterns indicated that animals at both sites eventually settled in areas where boulders were relatively dense, which may explain the similarity between population-level step lengths in Season 2. At a meso scale, the three-fold larger mean home range size of upper-site Hellbenders in Season 2 may also be explained by the patchy distribution of boulders there. Density of coarse substrate can directly influence the number of interstitial spaces that provide habitat for Hellbender prey (Townsend et al., 1997). Therefore, the relatively low density of coarse substrate may have increased home range size requirements of upper-site Hellbenders. Finally, at the broadest scale, the nearly three-fold larger extent of core habitat and dense arrangement of boulders at the lower site were associated with 20% higher release site fidelity and 1.5-fold higher annual survivorship (Bodinof et al., in press). Lower-site core habitat attributes appeared to allow longer-distance dispersals and longer dispersal windows, while avoiding mortality associated with core habitat abandonment. Although the net dispersal direction of most Hellbenders was directed downstream, we wish to emphasize the fact that upstream-directed movements at the daily scale (i.e., step lengths) were common, and we observed no obvious association between the relative point of release within core habitat and dispersal direction or release site fidelity of individuals. We recognize that we only compared movements between two sites, but speculate that the quality of habitat encountered during daily movements (within a 5-m radius) and extent of suitable habitat may be important determinants of dispersal

distance, direction, and ultimately release site fidelity. We recommend prioritizing release sites where the extent of suitable cobble–boulder substrate is maximized.

In addition to habitat, season of release may be an important consideration when translocating Hellbenders. For example, Hellbenders released in spring were more likely to disperse long distances (~50 m), which may reduce release site fidelity at sites where suitable habitat covers a relatively small extent (e.g., upper site). However, our sample size for both summer and autumn release cohorts was small, and longer-term monitoring may have revealed additional core habitat abandonment, especially for autumn-released Hellbenders, which tended to increase their home range (i.e., continued exploration) following winter. Similar to our findings, autumn-released captive-reared Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) exhibited smaller home ranges prior to winter than summer-released snakes (King et al., 2004), suggesting cooling temperatures may reduce herpetofauna movements and delay exploration and settlement in the wild. In addition to delayed dispersal, King et al. (2004) also noted lower survivorship in autumn-released snakes. We were unable to link season of release to survival probability, though one autumn-released Hellbender from our study settled in an area where microhabitat remained stable at low flows (i.e., autumn) but was heavily disturbed during a high-discharge event in spring, resulting in death when the used boulder was buried by bedload (Bodinof et al., in press). Releasing Hellbenders in spring or early summer, when discharge tends to be highest, may discourage settlement in unstable microhabitat. Additionally, spring or summer release would avoid potential disturbance or risks of injury due to conspecific aggression and defense of rock shelters associated with breeding in autumn (Smith, 1907). Collectively, we suggest releasing Hellbenders in spring or early summer, but acknowledge that more work is needed to determine how season of release may influence Hellbender translocation success.

Although long-term success of wildlife translocations ultimately relies on survival and reproduction of animals in the wild,

proximate causes of failure often include animal movements that prevent initial establishment of a population (Armstrong and Seddon, 2008; Germano and Bishop, 2009). We examined movement as one aspect of translocation success for captive-reared Ozark Hellbenders. Collectively, Hellbenders in our study exhibited movement indicative of short-term exploration followed by more permanent settlement, and fine-scale site fidelity typical of wild conspecifics. Our findings suggest that captive-rearing and translocation may be useful for augmenting populations where suitable habitat exists. However, we also recognize that factors such as the genetic structure of translocated populations and long-term stability of habitat within release sites have the potential to influence translocation success regardless of animal movement tendencies, and should be carefully considered when determining appropriate management strategies for particular species.

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