Freshwater Biology

Freshwater Biology (2012) **57,** 178–192 doi:10.1111/j.1365-2427.2011.02697.x

APPLIED ISSUES

Habitat attributes associated with short-term settlement of Ozark hellbender (*Cryptobranchus alleganiensis bishopi*) salamanders following translocation to the wild

CATHERINE M. BODINOF*, JEFFREY T. BRIGGLER†, RANDALL E. JUNGE‡, JEFF BERINGER§, MARK D. WANNER‡, CHAWNA D. SCHUETTE‡, JEFF ETTLING‡ AND JOSHUA J. MILLSPAUGH*

*Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO, U.S.A.

†Missouri Department of Conservation, Jefferson City, MO, U.S.A.

‡Saint Louis Zoological Park, Saint Louis, MO, U.S.A.

§Missouri Department of Conservation, Columbia, MO, U.S.A.

SUMMARY

1. Organisms associated with lotic systems rank among the most threatened because of global change. Although translocation is being increasingly applied as a conservation strategy, most studies have focused on survival and recruitment of individuals, and few have attempted to identify how habitat attributes influence short-term settlement of animals during the critical post-release period.

2. We demonstrate the application of resource selection modelling in an information theoretic framework to identify release-site characteristics that will increase the likelihood of settlement for a fully aquatic benthic stream salamander, the Ozark hellbender (*Cryptobranchus alleganiensis bishopi*). We fit discrete choice models using data from 29 radio-tagged hellbenders that were translocated to two sites in the North Fork of the White River (NFWR), Missouri (U.S.A.). We defined resource availability at two spatial scales (stream reach and home range) and quantified abiotic habitat attributes at 3181 salamander locations and 6329 random available locations collected between May 2008 and August 2009.

3. At both sites and spatial scales, a single model received substantially greater support (0.96–1.00 of total model weight) than all other models, and top-ranked models were similar in form and predictive ability. At both spatial scales, selection was positively influenced by the presence of cobble-boulder substratum relative to bedrock and finer substrata. We also noted a negative interactive effect between distance to the nearest substratum particle large enough to provide cover (i.e. at least one axis ≥15 cm in length) and an increase in either a direct or relative (i.e. pool, run, and riffle) measure of water velocity.

4. Collectively, salamanders released in our study selected resources indicative of long-term benthic microhabitat stability. However, despite strong selection of cobble-boulder substratum, 8% (282 of 3181) of captive-reared hellbender locations occurred in bank crevices and root masses. Although several studies have reported the importance of near bed hydraulics in determining occurrence of stream macroinvertebrates, our findings are the first to indicate that spacing among cobble-boulder substrata may be important for hellbenders.

5. To increase the likelihood of short-term settlement of captive-reared hellbenders in the wild, we recommend prioritising release sites where the average distance between cobble-boulder particles within habitat patches is minimised. In general, average spacing among cobble and boulder substrata should be <1 m in habitat patches where mean benthic water velocity exceeds 0.1 m s^{-1},

---

Correspondence: Catherine M. Bodinof, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 ABNR, Columbia, MO 65211, U.S.A. E-mail: cathybodinof@gmail.com

and <0.5 m where water velocity approaches 0.30 m s^{-1}. Based on home range sizes of captive-reared Ozark hellbenders, the collective extent of suitable cobble-boulder habitat patches within release sites should approximate at least 10 m^2 per salamander released.

Keywords: *Cryptobranchus alleganiensis*, release site suitability, resource selection, substratum, translocation

Introduction

Running water habitats are among the most imperilled on Earth, as a result of impoundment, exploitative water withdrawal, chemical contamination, siltation, introduction of non-native species and potential climate change (Benke, 1990; Ricciardi & Rasmussen, 1999; Malmqvist & Rundle, 2002; Heino, Virkkala & Toivonen, 2009). Not surprisingly, fauna associated with lotic systems typically rank among the most threatened taxa globally (Allan & Flecker, 1993). Studies have identified that in North America alone, 39% of known freshwater fishes (Jelks *et al*., 2008), 76% of known mussel species (Williams *et al*., 1993) and 48% of crayfish species (Taylor *et al*., 1996) require some level of protection. Among amphibians, which are one of the most threatened taxa globally, 62% of species associated with flowing water are currently experiencing rapid decline (Stuart *et al*., 2004). In response to threats re-introduction, repatriation and managed relocation (collectively 'translocation programs') are expected to be increasingly applied conservation strategies for lotic species (Olden *et al*., 2010).

The success of any animal translocation relies on the quality of habitat where animals are released (Armstrong & Seddon, 2008). This may be especially true for lotic species, many of which exhibit limited mobility (e.g. mussels, crayfishes, amphibians and some fishes), that are restricted to the longitudinal gradient of the stream where they are released. While survival may be the proximate determinant of persistence of a translocated population, persistence may ultimately depend on habitat that influences post-release movements, dispersal, settlement of individuals and thus establishment of a population in the wild (Armstrong & Seddon, 2008). For example, long-distance dispersals and high rates of movement in search of habitat matching a specific template can increase risk of predation and decrease body condition of recently translocated animals during the critical post-release phase, thereby lowering survival rates (Stamps & Swaisgood, 2007).

Focused monitoring and testing of *a priori* hypotheses concerning how habitat attributes may influence settlement of translocated animals can improve our ability to identify suitable release sites and therefore increase translocation success (Armstrong & Seddon, 2008). Wildlife resource selection studies assume that animals disproportionately use specific resources compared with what is available (Cooper & Millspaugh, 1999), presumably to increase fitness. Translocated animals are unique because they lack prior knowledge of release sites, and post-release selection may be influenced by conditions of captive rearing, attributes of a native range (Rittenhouse *et al*., 2007; Rust, 2010) or primitive instincts (Wiens, 1970, 1972). Therefore, quantifying resource selection patterns of translocated populations can help define objective criteria for selecting release sites that will increase the likelihood that translocation subjects will quickly settle and begin contributing to population establishment. Multiple studies have evaluated resource selection of translocated mammal (Anderson *et al*., 2005; Oakleaf *et al*., 2006; Jachowski *et al*., 2011) and avian (Baxter *et al*., 2009; Joyce, 2009; Michel *et al*., 2010) populations. However, among translocations involving lotic species, post-release monitoring tends to focus largely on survival and recruitment, and associations between habitat and population persistence are rarely evaluated (Cope & Waller, 1995), or only evaluated *post-hoc* (Harig & Fausch, 2002; Porath *et al*., 2010).

One lotic species that is undergoing precipitous declines throughout its range is the hellbender, *Cryptobranchus alleganiensis* Daudin (Mayasich, Grandmaison & Phillips, 2003; Wheeler *et al*., 2003; Foster, Mcmillan & Roblee, 2009). Hellbenders are fully aquatic, large (up to 74 cm), long-lived benthic salamanders (over 30 years) that occur in cool streams where there is a prevalence of large rocks for cover and crayfish for prey (Nickerson & Mays, 1973a, b; Taber, Wilkinson & Topping, 1975; Williams *et al*., 1981). Two subspecies of hellbender exist. The eastern hellbender (*C. a. alleganiensis*) occurs through portions of the Susquehanna, Tennessee, Ohio and Mississippi River drainages from New York south to Georgia, and in a disjunct portion of the Mississippi River drainage in south central Missouri. The Ozark hellbender (*C. a. bishopi* [Grobman, 1943]) is endemic to the Black and White river drainages of extreme southern Missouri and northern Arkansas. While hellbender declines have been noted throughout the species' range (Federal Register, 2010), both eastern and Ozark hellbenders have declined by an average of 77% in Missouri alone since the mid-1980s (Wheeler *et al*., 2003). Drivers of hellbender declines may include illegal harvest (Nickerson & Briggler, 2007), habitat disturbance, degraded water quality (Briggler *et al*., 2007), introduced predators (Gall & Mathis, 2010) or disease (Briggler, Larson & Irwin, 2008; Bodinof *et al*., 2011). Several agencies are considering captive rearing and translocation as a management strategy to improve wild hellbender populations. However, no studies have evaluated how captive-reared hellbenders might respond to translocation.

We demonstrate the application of resource selection modelling to identify release-site characteristics that will increase the probability of translocation subjects settling within release sites, using captive-reared Ozark hellbenders released as part of a pilot attempt to augment wild populations in one Missouri stream. Specifically our objectives were to (i) identify abiotic resource attributes associated with locations selected by captive-reared Ozark hellbenders post-release and (ii) define objective criteria for identifying fine scale habitat characteristics that will increase the probability of captive-reared Ozark hellbenders settling within a release site.

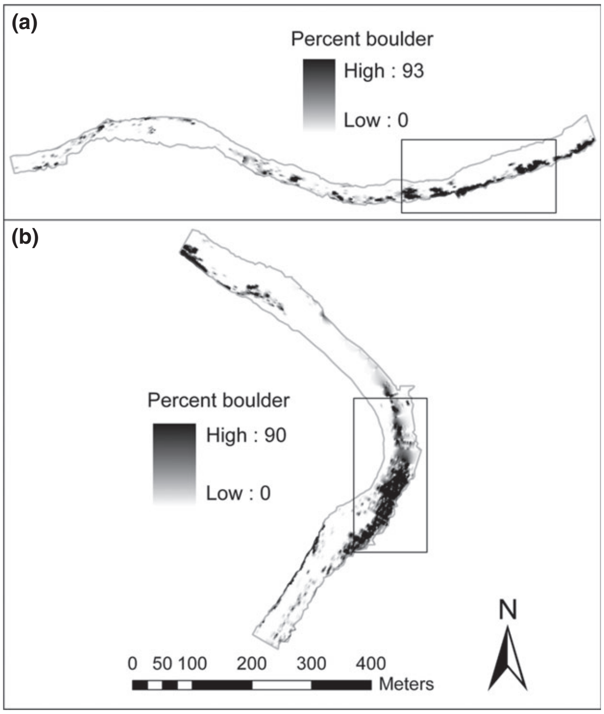

Fig. 1 Core habitat (boxes) within the upper (a) and lower (b) sites on the North Fork of the White River, Missouri, where captive-reared *Cryptobranchus alleganiensis bishopi* were released, 2008–2009. Note the patchier, smaller extent of boulder cover within upper site core habitat.

Methods

Study area

Our study was conducted along the North Fork of the White River (NFWR), a seventh order, primarily spring-fed stream, originating in southern Missouri. The NFWR flows south for approximately 167 km before entering Norfork Reservoir near the Arkansas border (U.S.A.). In Missouri, the NFWR catchment encompasses 3597 km^2 of land characterised by karst topography and classified by the Missouri Department of Conservation as crop/grassland (37.5%), forest/woodland (61.9%) and urban (0.1%) land use (http://extra.mdc.mo.gov/fish/watershed/northfrk/contents/).

Our study consisted of two sites (hereafter upper and lower) in the NFWR, separated by approximately 17 km of stream. We choose not to reveal the discrete location of study sites because of threats of illegal collecting and the current status of hellbenders in Missouri. We based our selection of translocation sites on the presence of boulders and an apparent abundance of crayfish for prey. Each site was approximately 1 km long and contained at least one relatively large patch of cobble and boulder that we defined as 'core habitat' (Fig. 1). Clusters of boulder appeared patchy and largely overlapped bedrock with deep crevices within upper site core habitat, while boulders were densely arranged, covered a greater extent and bedrock crevices were virtually absent within lower site core habitat. Core habitat at both sites was bordered up- and downstream by extensive (>200 m long) gravel-pebble beds. Prior surveys had yielded fewer than 10 wild hellbenders in core habitat of each site. Therefore, resident density was estimated to be extremely low compared with historical accounts from the NFWR (Nickerson & Mays, 1973a,b). Random sampling of runs and riffles (<1 m deep) using a 1-m kick-seine technique (Mather & Stein, 1993) in August 2008 indicated that crayfish (prey) densities were similar between sites (upper site = 12.16 ± 2.4 crayfish m^{-2} SE; lower site = 12.61 ± 1.52 crayfish m^{-2} SE).

Study animals

We monitored 36 captive-reared juvenile Ozark hellbenders that were released to bolster remnant wild populations. Salamanders were hatched from eggs collected from the NFWR in 2002 (S. Unger, unpubl. data), and were reared in captivity from 2003 until 2008 at the Saint Louis Zoo's Ron Goellner Center for Hellbender Conservation. We lined captive enclosures with gravel, cobble and boulder substrata, and circulated cool oxygenated water to mimic wild conditions. Before release, we surgically implanted each salamander with Sirtrack Limited model RVI 118 or RVI 218 radio transmitters permitting the transmitter weight was ≤5% salamander mass. At surgery, mean mass of salamanders was 202 ± 9 g SE (range = 142–334 g), mean total length was 319 ± 4 mm SE (range = 285–368 mm) and genders were unknown. We released salamanders 14–28 days after surgery unless we observed rupturing of sutures, in which case we repaired sutures and held individuals for 14–28 additional days prior to release. We randomly selected 18 salamanders to be released under pre-selected boulders within core habitat of each study site over four discrete events between May and October 2008.

Sampling of used and available resources

To account for variation in selection across all times of day, we systematically located each salamander every 32 ± 4 h (approximately five locations per week) between 19 May 2008 and 14 November 2008, and between 26 March 2009 and 18 August 2009. Between 14 November 2008 and 25 March 2009 (hereafter winter), we located salamanders approximately once per week but did not include winter observations in our resource selection analyses. We identified salamander locations by wading or canoeing (if water depth ≥1.5 m) and homing procedures (White & Garrott, 1990) using a three element Yagi antenna and an Advanced Telemetry Systems (Isanti, MN, U.S.A.) receiver (model R2000, R4000 or R410). Homing allowed us to identify discrete cover resources, such as rocks or root masses, and allowed us to document fine scale (≥0.30 m) movement between objects. When we could not distinguish the used cover resource by homing, we confirmed locations visually by snorkelling or with an Aqua-Vu® SV 100 (Outdoor Insights Inc., Crosslake, MN, U.S.A.) camera.

We quantified availability of resources at two spatial scales, including within the immediate reach (50–100 m radius) and within the immediate vicinity representative of a typical home range [5 m radius (e.g. 79 m^2 as per Peterson & Wilkinson, 1996)]. Cooper & Millspaugh (1999) emphasise the importance of defining availability based on accessibility defined by movement constraints for a particular species. While hellbenders are capable of travelling long distances (>100 m) up- and downstream (Gates *et al.*, 1985), such lengthy movements are rare (Nickerson & Mays, 1973a, b; C. Bodinof, unpubl. data). Typically, hellbender space use is characterised by high fidelity to a relatively small patch of habitat (Hillis & Bellis, 1971). Therefore, the broadest spatial scale we considered (hereafter reach scale) reflected availability within an area accessible to each salamander, based on the time interval between sequential relocations, but that likely occurred outside of the home range. The finest spatial scale (hereafter home range scale) reflected an area that was accessible over a shorter temporal scale and more likely to be encountered during typical movements within a home range. Each time we located a salamander (except during winter) we identified one random available location at the reach scale and one at the home range scale, based on a random azimuth (selected with replacement) and a random distance between 50 and 100 m (reach scale) or 0.5 and 5 m (home range scale). If the available location fell outside of the river corridor (e.g. on dry land), we selected a new random azimuth and distance until the location fell within the wetted river channel.

At each used and available location, we measured eight abiotic resource attributes that we hypothesised might influence Ozark hellbender selection (Table 1). We recorded the size class (Wentworth, 1922) of the substratum particle first encountered by a metre-stick placed vertically over used locations or placed blindly at available locations. If salamanders were located ‘out’ from cover, we recorded size class of the substratum the majority of the animal was resting on. When salamanders were located under objects other than rocks (e.g. bank crevices), we recorded size class of the first particle encountered within the cavity being used. We recorded the dimensions

Table 1 Covariates used in captive-reared *Cryptobranchus alleganiensis bishopi* resource utility models

Variable	Description	Adjusted value
Bed_{sub}	Bedrock	Bed_{sub}
$Coarse_{sub}$	Coarse substratum [cobble and boulder as per Wentworth (1922)]	$Coarse_{sub}$
$Size_{coarse}$	Size (width) of coarse substratum (cm), other substrata = 0	$Size_{coarse} + 0.01$
$Dist_{cover}$	Distance to substratum with at least one axis ≥15 cm (m)	$Dist_{cover} + 0.01$
Pool	Pool	Pool
Run	Run	Run
$Velocity_{ave}$	Average benthic water velocity m s^{-1} over 10 s	$Velocity_{ave} + 0.01$
$Velocity_{max}$	Maximum benthic water velocity m s^{-1} over 10 s	$Velocity_{max} + 0.01$
Depth	Water depth (cm)	Depth
Temp	Benthic temperature (°C)	Temp
I	Random effect for individual	

(length cm × width cm × depth cm) of cobble and boulder but not smaller particles and defined size ($\text{size}_{\text{coarse}}$) of these particles by width (i.e. the longest axis perpendicular to the maximum diameter of substratum). Based on the minimum size of substratum used by wild Ozark hellbenders during surveys conducted by the Missouri Department of Conservation, we defined 'cover' as any substratum particle with at least one axis ≥15 cm. We measured 'distance to cover' ($\text{dist}_{\text{cover}}$) as the shortest distance (m) between the edge of the substratum particle at each location and the edge of the nearest 'cover' using a tape measure (when ≤15 m) or handheld Nikon Prostaff laser rangefinder (Nikon Inc., Mellville, NY, U.S.A.) (when >15 m). When salamanders were located under an object that touched 'cover', distance was recorded as 0 m. We measured maximum ($\text{velocity}_{\text{max}}$) and average benthic water velocity ($\text{velocity}_{\text{ave}}$) (m s^{-1}) over approximately 10 s with a hand-held flow meter (Global Water Instrumentation Inc., Gold River, CA, U.S.A.) placed immediately upstream of the substratum particle at each location. We recorded meso-habitat at each location, as pool (little to no water movement or circulating flow), run (slow to swift-moving water with a smooth surface) or riffle (swift-moving water with a disrupted surface). Because our definitions of meso-habitat were somewhat subjective, we quantified mean benthic water velocity within each meso-habitat for each site separately using data collected at random available locations. We measured water depth to the nearest cm immediately downstream of the substratum particle at each location and measured water temperature at the benthic level to the nearest 0.1 °C using a ClineFinder™ digital thermometer (Catalina Technologies Inc., Tucson, AZ, U.S.A.).

Model development

We developed 15 *a priori* literature-based models representing our hypotheses of how abiotic resource attributes influence the utility of a resource for hellbenders, and thus selection (Table 2). Models included various combinations

Table 2 *A priori* resource utility models developed for captive-reared *Cryptobranchus alleganiensis bishopi*

Hypothesis	Model structure
Substratum	
(1) Positive influence of coarse substratum and bedrock	$=\beta_1(\text{bed}_{\text{sub}}) + \beta_2(\text{coarse}_{\text{sub}}) + \beta_3(\text{I})$
(2) Positive influence of size of coarse substratum and negative influence of distance to cover	$=\beta_1(\text{coarse}_{\text{sub}}) + \beta_2(\text{dist}_{\text{cover}}) + \beta_3(\text{I})$
(3) Positive influence of a mid-range of sizes of coarse substrata	$=\beta_1(\text{size}_{\text{coarse}}) + \beta_2(\text{size}^2_{P\text{coarse}}) + \beta_3(\text{I})$
(4) Positive influence of coarse substratum and bedrock; negative exponential influence of distance to cover	$=\beta_1(\text{bed}_{\text{sub}}) + \beta_2(\text{coarse}_{\text{sub}}) + \beta_3(\exp(-\text{dist}_{\text{cover}})) + \beta_4(\text{I})$
(5) Positive influence of coarse substratum; greater negative influence of distance to cover on the utility of coarse substratum relative to bedrock	$=\beta_1(\text{bed}_{\text{sub}}) + \beta_2(\text{coarse}_{\text{sub}}) + \beta_3(\text{dist}_{\text{cover}})$ $+ \beta_4(\text{bed}_{\text{sub}} \times \text{dist}_{\text{cover}}) + \beta_5(\text{coarse}_{\text{sub}} \times \text{dist}_{\text{cover}}) + \beta_6(\text{I})$
Hydraulics	
(6) Positive influence of riffles	$=\beta_1(\text{pool}) + \beta_2(\text{run}) + \beta_3(\text{I})$
(7) Positive influence of riffles and low temperature	$=\beta_1(\text{pool}) + \beta_2(\text{run}) + \beta_3(\text{T}) + \beta_4(\text{I})$
(8) Positive influence of a mid-range of depths	$=\beta_1(\text{depth}) + \beta_2(\text{depth}^2) + \beta_3(\text{I})$
(9) Negative influence of high temperatures and high average benthic water velocity	$=\beta_1(\text{temp}) + \beta_2(\exp(-\text{velocity}_{\text{ave}})) + \beta_3(\text{I})$
(10) Negative influence of high temperature and high maximum benthic water velocity	$=\beta_1(\text{temp}) + \beta_2(\exp(-\text{velocity}_{\text{max}})) + \beta_3(\text{I})$
Substratum + Hydraulics	
(11) Positive influence of coarse substratum and bedrock; negative influence of distance to cover as maximum benthic water velocity increases	$=\beta_1(\text{bed}_{\text{sub}}) + \beta_2(\text{coarse}_{\text{sub}}) + \beta_3(\text{velocity}_{\text{max}})$ $+ \beta_4(\text{dist}_{\text{cover}}) + \beta_5(\text{velocity}_{\text{max}} \times \text{dist}_{\text{cover}}) + \beta_6(\text{I})$
(12) Positive influence of coarse substratum, bedrock, and average benthic water velocity; negative influence of distance to cover	$=\beta_1(\text{bed}_{\text{sub}}) + \beta_2(\text{coarse}_{\text{sub}}) + \beta_3(\text{velocity}_{\text{ave}}) + \beta_4(\text{dist}_{\text{cover}}) + \beta_5(\text{I})$
(13) Positive influence of coarse substratum and bedrock; negative influence of distance to cover in riffles and runs, but reduced effect of distance to cover in pools	$=\beta_1(\text{bed}_{\text{sub}}) + \beta_2(\text{coarse}_{\text{sub}}) + \beta_3(\text{pool}) + \beta_4(\text{run})$ $+ \beta_5(\text{dist}_{\text{cover}}) + \beta_6(\text{pool} \times \text{dist}_{\text{cover}}) + \beta_7(\text{run} \times \text{dist}_{\text{cover}}) + \beta_8(\text{I})$
(14) Increasing negative influence of distance to cover as maximum benthic water velocity increases	$=\beta_1(\text{dist}_{\text{cover}}) + \beta_2(\text{velocity}_{\text{max}}) + \beta_3(\text{dist}_{\text{cover}} \times \text{velocity}_{\text{max)}} + \beta_4(\text{I})$
(15) Positive influence of size of coarse substratum; increasing negative influence of distance to cover as maximum benthic water velocity increases	$=\beta_1(\text{size}_{\text{coarse}}) + \beta_2(\text{dist}_{\text{cover}}) + \beta_3(\text{velocity}_{\text{max}})$ $+ \beta_4(\text{dist}_{\text{cover}} \times \text{velocity}_{\text{max}}) + \beta_5(\text{I})$

of two categorical and six continuous variables and all included a random effect to account for variability in selection among individuals. To increase parsimony (Burnham & Anderson, 2002) and reduce the number of parameters in our models, we collapsed substratum type into three categories which included coarse ($\text{coarse}_{\text{sub}}$; boulder and cobble), fine (fine_{sub}; pebble, gravel, sand and silt) and bedrock (bed_{sub}). Dummy variable coding for categorical variables required that one category be removed from each model as a reference category for comparison. We removed the fine substratum category as reference for substratum type and removed the riffle category as a reference category for meso-habitat. For covariates that were often represented by values of 0, we added a constant of 0.01 to each value (Table 1). Rather than assuming linear relationships between selection and each continuous variable, we plotted data from used locations prior to model fitting to determine whether evidence existed to support nonlinear relationships. We considered a quadratic form ($\beta_1 x_1 + \beta_2(x_2^2)$) of coarse substratum size, water temperature and water depth; and a negative exponential form ($\beta_1 x_1 + \beta_2(\exp(-x_2))$ of distance to cover and average and maximum benthic water velocity (Table 2).

Models were grouped under two categories of factors hypothesised to influence resource utility for hellbenders, including substratum and hydraulics. Because wild hellbenders are known to occasionally use bedrock (Petokas *et al.*, 2006) but are predominantly associated with boulders, we included a substratum model hypothesising that presence of coarse substratum would positively influence selection. Hellbenders typically remain hidden, but occurrence and abundance has been suggested to be related to the number (Nickerson & Mays, 1973a) and size (Hillis & Bellis, 1971) of boulders present. Therefore, we included models containing variables for the type or size of substratum, as well as 'distance to cover'. Additionally, we included a model hypothesising that 'distance to cover' might influence the utility of each substratum differently [e.g. ($\text{dist}_{\text{cover}} \times \text{bed}_{\text{sub}}$) + ($\text{dist}_{\text{cover}} \times \text{coarse}_{\text{sub}}$)]. Because wild hellbenders are typically associated with cool, swift-moving water (Bishop, 1941; Williams *et al.*, 1981), we included a hydraulic model suggesting riffles, high benthic water velocities and low temperatures would be positively associated with selection, and models suggesting that a mid-range of depths would increase selection probability. Finally, because studies involving benthic macro-invertebrates demonstrate the strong influence of water velocity and substratum on species distribution (Statzner & Higler, 1986), we developed models that considered independent and interactive relationships between substratum and hydraulics covariates. For example, in one model, we hypothesised that coarse substratum would positively influence utility, but that increasing 'distance to cover' would reduce the utility of coarse substratum in riffles and runs where benthic shear stress (lateral force of flowing water) was expected to be relatively high (Table 2).

Model fitting and selection

We used discrete choice modelling to evaluate resource selection by hellbenders. In wildlife resource selection studies, discrete choice models allow calculation of the probability of an individual selecting a resource based on its relative 'utility', where utility is a function of attributes offered by a particular resource (Cooper & Millspaugh, 2001). Discrete choice modelling is similar to logistic regression; in that, used locations are compared with available locations, except that data from used and available points are paired to account for changes in availability over space or time. The unique pairing of used and available resources, offered by discrete choice methods, allowed more accurate estimation of resource availability in light of the fluctuating abiotic conditions of lotic environments and limited mobility of hellbenders. When fitting discrete choice resource utility models, each sample consists of a 'choice set' that includes data from a used location and one or more locations deemed available at the time the resource was used, and parameters are estimated using iterative maximum likelihood methods (Cooper & Millspaugh, 2001). After fitting models, the utility of a particular resource can be expressed as:

$$\text{Utility} = B'X + \text{e} = \beta_1 x_1 + \beta_2 x_2 \ldots \beta_m x_m + \text{e}$$

where B′ is a vector length of *m* estimable parameters and X is a vector of *m* measurable attributes (e.g. substratum type and water velocity) of the resource (Cooper & Millspaugh, 1999, 2001). Following, the relative utility and therefore the probability of an individual selecting a resource can be expressed as:

$$P(A) = \left(\frac{\exp(\text{Utility}_A)}{\sum\limits_{A \to i} \exp(\text{Utility}_i)} \right)$$

where *A* is one resource of *i* resources available to an individual (Cooper & Millspaugh, 1999). Cooper & Millspaugh (1999) provide further details on discrete choice model fitting, application and interpretation.

We fit hypothesised resource utility models to our data, with each choice set consisting of one used and one corresponding available observation. Before model fitting, we removed data from individuals with ≤20 used observations over the course of the study. We fit models separately for each study site and each spatial scale using PROC MDC in SAS© (SAS Institute, Cary, NC, U.S.A.). We used Akaike's Information Criterion adjusted for small sample size (AIC_c) (Burnham & Anderson, 2002) to rank each model in the candidate set. We defined the top model as the model assigned ≥90% of the AIC_c model weight (w_i; Burnham & Anderson, 2002). We report all mean values and model parameter coefficients ± 1 SE.

Model validation

Model ranking within an AIC framework identifies the most supported models in the candidate set, but provides no measure of model accuracy. To assess predictive ability of each top-ranked model, we used k-fold cross validation (Boyce *et al.*, 2002). We first randomly selected 80% of our choice sets (maintaining the 1 : 1 ratio of used to available resource data) as 'training data' and designated the remaining 20% of the choice sets as a 'test set'. We replicated this random separation five times for each top-ranked model and refit each model five times, using each replicate of training data. We used the newly fitted models to estimate the relative probability of selection for resources within each choice set in test data sets. We assessed model performance by identifying the percentage of used observations that were correctly predicted (i.e. had a relative probability of selection >0.5), after pooling all test sets for each model.

Results

We collected 1387 reach-scale and 1416 home range-scale choice sets for 15 salamanders at the upper (patchy boulder) site, and 1761 reach-scale and 1765 home range-scale choice sets for 14 salamanders at the lower (dense boulder) site. The mean number of reach-scale choice sets collected per salamander was 92 ± 16 at the upper site and 126 ± 14 at the lower site. Although we did not include winter observations in our resource selection analysis, none of the salamanders monitored moved to new areas of the stream during winter.

During our study, mean daily discharge of the NFWR averaged 17.66 ± 12.63 m^3 s^{-1} [range = 8.83–156.59 (USGS gage 07057500, NFWR near Tecumseh)]. Within each meso-habitat class, mean benthic velocity had low variability and was similar among sites, with the lowest values in pools and the highest in riffles (Table 3). However, we were unable to sample benthic water velocities when discharge exceeded about 28 m^3 s^{-1}. High flows exceeding 28 m^3 s^{-1} typically lasted <48 h but included two events in September 2008 and two events in early spring 2009 (hydrograph available through http://waterdata.usgs.gov).

Table 3 Mean benthic water velocity (m s^{-1}) of meso-habitats within upper and lower sites on the North Fork of the White River, MO, U.S.A., 2008–2009, based on data collected at random available locations within reach-scale choice sets from 19 May–14 November 2008 and from 26 March 2009–19 August 2009

	Upper site			Lower site		
	$\bar{x}$*	SE†	n‡	$\bar{x}$*	SE†	n‡
Pool	0.00	0.00	332	0.00	0.00	204
Run	0.16	0.01	798	0.18	0.00	1001
Riffle	0.32	0.01	250	0.34	0.01	551

*Mean benthic water velocity (m s^{-1}).

†1 standard error.

‡Sample size.

We made 262 observations (8% of salamander locations) of 10 salamanders (upper site: $n = 6$, lower site: $n = 4$) using cover other than rocky substratum. These included observations in bank crevices (upper site: $n = 20$, lower site: $n = 5$), root mass of water willow (*Justica americana* L. [Vahl.]) (upper site: $n = 9$, lower site: $n = 140$) and woody root wads of trees along the bank (upper site: $n = 2$, lower site: $n = 86$). Use of non-rocky resources usually lasted ≤14 days; however, one lower site male used a tunnel approximately 0.5 m long in *J. americana* root mass lined with sand and silt for over 1 year; and a lower site female used a cavity filled with cobble and sand among the roots of a living Sycamore (*Platanus occidentalis* L.) for ≥8 months. Because bank crevices and root masses with openings large enough for hellbenders were difficult to detect and extended outside of the main river channel, they were not encountered at randomly selected available locations. Moreover, as we were unable to sample the availability of root masses and bank crevices, they were not included as covariates in our models.

Hellbender selection

We observed no model selection uncertainty in AIC_c ranking of models ($w_i = 0.96$–1.0) and top-ranked models at both sites and spatial scales were similar in form (Tables S1 & S2). All four top models included covariates for substratum type; and an interaction between 'distance to cover' and either a direct ($velocity_{max}$) or relative (pool, riffle, run) measure of water velocity.

Captive-reared Ozark hellbender selection was positively associated with the presence of coarse substratum,

Table 4 Parameter estimates for top-ranked reach-scale resource utility models for captive-reared *Cryptobranchus alleganiensis bishopi* released at the upper and lower sites on the North Fork of the White River, MO, U.S.A., 2008–2009

Upper site				Lower site			
*β**	Estimate	SE[†]	e^x [‡]	*β**	Estimate	SE[†]	e^x [‡]
Bed$_{sub}$	2.0884	0.2217	8.0719	Bed$_{sub}$	0.8793	0.3786	2.4092
Coarse$_{sub}$	2.9319	0.2587	18.7630	Coarse$_{sub}$	2.9465	0.2414	19.0300
Pool	0.5494	0.2841	1.7322	Pool	1.3352	0.3274	3.8007
Run	0.1890	0.2467	1.2080	Run	−0.9353	0.2084	0.3924
Dist$_{cover}$	−0.2262	0.0798	0.7975	Dist$_{cover}$	−5.6258	1.4903	0.0036
Pool × dist$_{cover}$	−0.5910	0.2300	0.5537	Pool × dist$_{cover}$	4.6334	1.5039	102.8632
Run × dist$_{cover}$	−0.4634	0.1157	0.6291	Run × dist$_{cover}$	4.7622	1.4908	117.0030
I	1.0000			I	1.0000		

*Model parameter.
[†]1 standard error.
[‡]Odds ratio.

Table 5 Parameter estimates for top-ranked home range-scale resource utility models for captive-reared *Cryptobranchus alleganiensis bishopi* released at the upper and lower sites on the North Fork of the White River, MO, U.S.A., 2008–2009

Upper site				Lower site			
*β**	Estimate	SE[†]	e^x [‡]	*β**	Estimate	SE[†]	e^x [‡]
Bed$_{sub}$	1.8649	0.2075	6.4552	Bed$_{sub}$	1.1601	0.3703	3.1902
Coarse$_{sub}$	3.3986	0.2193	29.9221	Coarse$_{sub}$	3.3937	0.2061	29.7750
Velocity$_{max}$	−2.9636	0.5107	0.0516	Pool	1.9442	0.3517	6.9880
Dist$_{cover}$	−0.2892	0.0750	0.7488	Run	0.4074	0.3209	1.5029
Dist$_{cover}$ × velocity$_{max}$	0.5069	0.1492	1.6601	Dist$_{cover}$	−4.1448	1.0851	0.0158
I	1.0000			Pool × dist$_{cover}$	3.5441	1.0933	34.6080
				Run × dist$_{cover}$	3.7782	1.0913	43.7370
				I	1.0000		

*Model parameter.
[†]1 standard error.
[‡]Odds ratio.

and bedrock to a lesser degree, relative to fine substratum. Compared with fine substratum, odds ratios (e^{β}) indicated that the presence of bedrock increased the odds of selection by eight- (reach) and six-fold (home range) at the upper (patchy boulder) site; but by only two- (reach) and three-fold (home range) at the lower (dense boulder) site. Compared with fine substratum, coarse substratum increased the odds of selection 18 to 29-fold at the upper site and 19 to 29-fold at the lower site (Tables 4 & 5). While the presence of coarse substratum was associated with increased utility of a resource for hellbenders, we found no evidence that the size of coarse substratum influenced selection. For example, we observed no support for models including size$_{coarse}$ (e.g. Tables S1 & S2, model 15). Mean length (maximum diameter) of coarse substratum used by salamanders was 217 ± 8 cm (range = 21–915) at the upper site and 75 ± 1 cm (range = 20–300) at the lower site.

At both sites, there was a consistent negative association between the relative probability of selection and increasing 'distance to cover' (Figs 2–4). According to data collected at random available locations within our reach-scale choice sets, 'distance to cover' from coarse substratum within study sites averaged 0.59 ± 0.26 m [n = 100; upper (patchy boulder) site] and 0.35 ± 0.11 m [n = 319; lower (dense boulder) site]. However, among used locations, where salamanders were located under coarse substratum, 75% (upper site) and 74% (lower site) were 0 m from cover.

The interaction between 'distance to cover' and meso-habitat [(dist$_{cover}$ × pool) + (dist$_{cover}$ × run)] in three top-ranked models (upper site reach, lower site reach and lower site home range) indicated that the effect of increasing 'distance to cover' varied in intensity among meso-habitats and study sites. For example, the relative probability of salamanders selecting resources in runs at the upper site, when 'distance to cover' was 0 m, was 1.5–1.6 times greater than when 'distance to cover' was just 1.0 m, while the utility of resources in pools and riffles were less affected (Fig. 2). The effect of increasing

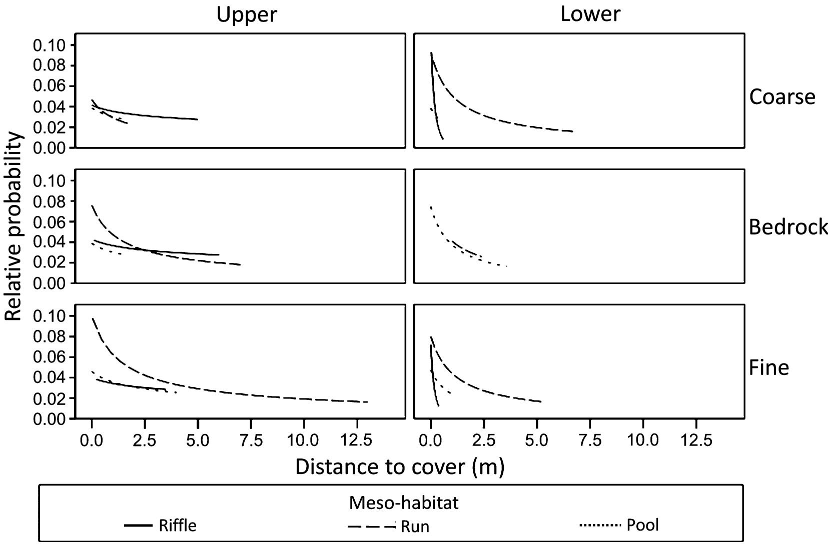

Fig. 2 Reach-scale resource selection functions, based on top-ranked reach-scale models, for captive-reared *Cryptobranchus alleganiensis bishopi* released at the upper and lower sites in the North Fork of the White River, MO, U.S.A., 2008–2009. Functions indicate the relative (not absolute) probability of selecting a resource based on the attributes offered by that resource and attributes offered across the range of resources hellbenders were observed using. Comparisons among relative probability of selection values are limited to within distinct scenarios (i.e. coarse substratum and riffle), but are not comparable among meso-habitats, substratum types or study sites.

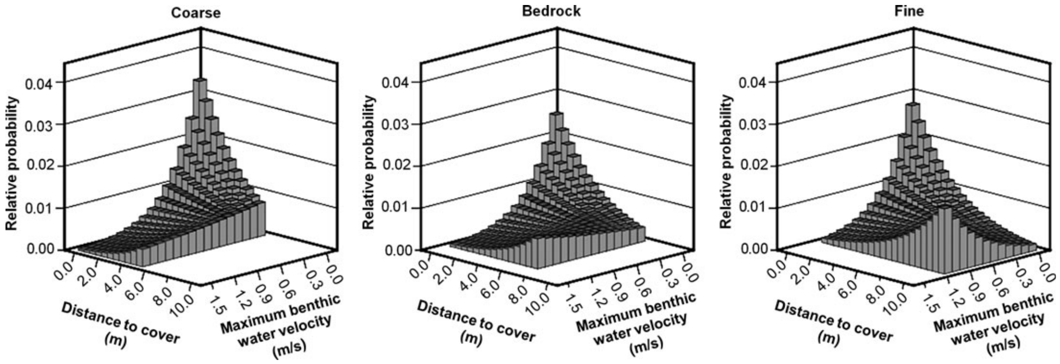

Fig. 3 Home range-scale resource selection functions, based on the top-ranked home range-scale model, for captive-reared *Cryptobranchus alleganiensis bishopi* released at the upper site in the North Fork of the White River, MO, U.S.A., 2008–2009. Functions indicate the relative (not absolute) probability of selecting a resource based on the attributes offered by that resource and attributes offered across the range of resources hellbenders were observed using. Comparisons among relative probability of selection values are comparable within, but not among, substratum types.

'distance to cover' was more intense throughout the lower site, particularly in riffles. The relative probability of salamanders selecting a resource in riffles at the lower site was 1.3–7.3 times greater when distance to cover was 0 m, than when 'distance to cover' was just 0.5 m (Fig. 2).

Unlike other models, an interaction between two continuous variables ($\text{dist}_{\text{cover}} \times \text{velocity}_{\text{max}}$) appeared in the top-ranked home range-scale model for upper (patchy boulder) site salamanders. The function indicated that the relative probability of salamanders selecting a resource when both 'distance to cover' and maximum benthic water velocity were zero exceeded the probability of selecting a resource when either parameter increased across the range of values that we observed salamanders using (Fig. 3).

Model validation

k-Fold cross validation of top-ranked models suggested that reach-scale models were slightly more accurate predictors of captive-reared Ozark hellbender resource selection. Reach-scale models accurately predicted use in 89% of upper site cases and in 91% of lower site cases. Home range-scale models accurately predicted 77% of upper site cases and 74% of lower site cases.

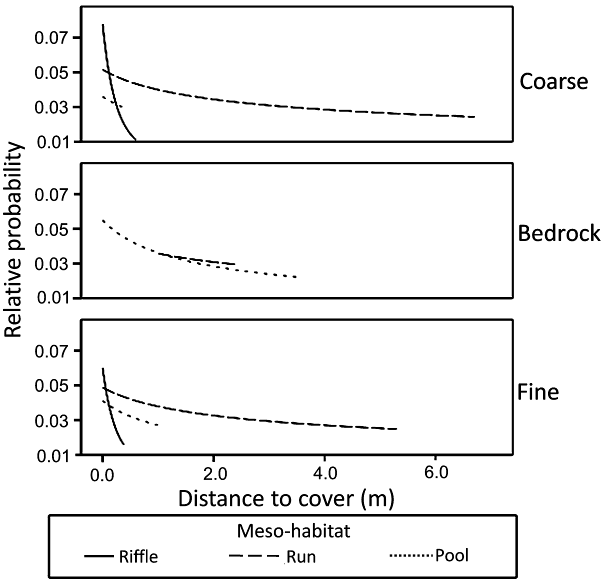

Fig. 4 Home range-scale resource selection functions, based on the top-ranked home range-scale model, for captive-reared *Cryptobranchus alleganiensis bishopi* released at the lower site in the North Fork of the White River, MO, U.S.A., 2008–2009. Functions indicate the relative (not absolute) probability of selecting a resource based on the attributes offered by that resource and attributes offered across the range of resources hellbenders were observed using. Comparisons among relative probability of selection values are limited to distinct scenarios (i.e. coarse substratum and riffle), but are not comparable among meso-habitats, substratum types, or study sites.

Discussion

Similar to relationships observed between substrata, water velocity and the zonation of benthic stream invertebrates (Statzner & Higler, 1986; Howard & Cuffey, 2003), fine scale resource selection of a large aquatic salamander was predicted based on substratum and water velocity characteristics. Our results provide strong support for the hypothesis that captive-reared Ozark hellbenders specialise in habitat containing coarse substratum, as we predicted based on habitat associations described for wild conspecifics (Nickerson & Mays, 1973b; Humphries & Pauley, 2005). Additionally, our study is the first to indicate that spacing between coarse substratum particles may considerably influence the utility of resources for these benthic stream salamanders. Despite hatching and rearing in captivity for over 5 years, salamanders released in our study selected resources indicative of benthic microhabitat stability. For long-lived, benthic stream species that rarely exhibit long-distance movements, short-term settlement may be largely influenced by fine scale habitat characteristics within release sites at the time of translocation, but persistence of the population may ultimately depend on factors influencing the long-term stability of benthic microhabitat, such as flow regime or anthropogenic modification of substratum composition.

Streambed substratum is known to influence the occurrence (Statzner & Higler, 1986; Usio, 2007; Murray & Innes, 2009), movements (Jaeger *et al.*, 2005) and survival (Berger & Gresswell, 2009) of stream-dwelling insects, mussels, crayfishes and fishes. Therefore, it is not surprising that coarse substratum was a major determinant of hellbender resource selection. Coarse substratum provides protective cover for hellbenders, which typically avoid light (Nickerson & Mays, 1973a), and habitat for prey including crayfish and small fish (Peterson, Reed & Wilkinson, 1989). Additionally, because 'critical shear stress' (the amount of energy required to move a particle) increases with particle size, coarse substratum represents relatively stable microhabitat within a lotic environment.

The potential for extremely high flow events, even of short duration, to limit the stability of microhabitat provided by coarse substratum, may explain why hellbender selection was improved when coarse substratum was present and 'distance to cover' was 0 m (i.e. two pieces of coarse substratum were touching). By defining the roughness coefficient, substratum can largely determine the 'shear stress' (lateral force of flowing water) and turbulence of benthic stream environments and therefore, the occurrence and movements of benthic species (Hoffman *et al.*, 2006). Hellbenders exhibit predominantly 'resistance' rather than 'resilience', life-history traits (Townsend, Dolédec & Scarsbrook, 1997), and habitat patches characterised by densely arranged coarse substratum can represent relatively secure and reliable resources in a dynamic stream environment. The increased turbulence and reverse flows that occur in the wakes of boulders (Bouckaert & Davis, 1998) may be important for retaining and circulating chemical cues that hellbenders rely on to locate prey and conspecifics during the breeding season (Bishop, 1941; Nickerson & Mays, 1973a). In addition, closely arranged coarse substratum directly increases the extent of protective cover for benthic organisms and can facilitate short-distance movements while avoiding prolonged exposure. As defined by our study, 'distance to cover' was one aspect of coarse substratum density (e.g. coarse substratum m^{-2}). Although we did not quantify density of coarse substratum, we speculate that the metric may be an even stronger predictor of salamander selection than 'distance to cover'. Regardless of the mechanism by which salamanders were benefited by closely arranged coarse substratum, there is strong quantitative evidence of its importance and we suggest that suitability of future release sites for captive-reared Ozark hellbenders be at least partially based on coarse substratum spacing. Release site suitability for other benthic stream species, especially organisms that exhibit 'resistance' life-history traits, may similarly depend on substratum type, arrangement and stability, and we encourage future studies to consider these aspects when evaluating potential release sites.

While captive-reared Ozark hellbenders exhibited resource selection patterns similar to wild conspecifics, they used a much wider variety of microhabitats than generally described for the species. Few studies have reported hellbender use of bedrock (Petokas *et al.*, 2006; Wheeler, 2007). However, our model parameter estimates indicated that bedrock positively influenced utility and may have been particularly important when coarse substratum was patchily distributed [i.e. upper site (Tables 4 & 5)]. We noted that bedrock crevices were also more prevalent at the upper site, while bedrock within the lower site was largely continuous (i.e. lacking crevices). Therefore, upper site bedrock may have simply been more hospitable to salamanders than lower site bedrock, and thus had a stronger positive influence on selection. In addition to considerable use of bedrock, nearly one-third of the captive-reared salamanders used bank crevices or root masses at least once. Although there are few reports of wild hellbenders using bank crevices (Peterson, 1988), their closest extant relatives, *Andrias sp.*, commonly den in stream banks, especially where rocky cover is reduced or absent (Kawamichi & Ueda, 1998; Wang *et al.*, 2004). Our findings indicate non-rocky microhabitats can provide at least a temporary surrogate to the interstitial spaces of coarse substratum for captive-reared Ozark hellbenders, and that use of these resources by wild hellbenders may be underestimated because of sampling bias.

Although minimising 'distance to cover' consistently increased the utility of a resource for captive-reared Ozark hellbenders, interactions in our models indicated that the utility of meso-habitats where mean benthic water velocity exceeded 0.10 m s^{-1} (Table 3) may be limited by 'distance to cover'. While the influence of 'distance to cover' on the relative probability of salamanders selecting sites within pools or runs at either site was somewhat similar, we noted a large disparity in the effect of 'distance to cover' on riffles among sites (Figs 2 & 4). One possible explanation for this difference may be the greater prevalence of bedrock ledges within upper site riffles, which were not considered when quantifying 'distance to cover'. Bedrock ledges may have increased the extent of protective cover and reduced shear stress similar to objects that met our definition of 'cover'. Our failure to consider bedrock, bank crevices or root masses as 'cover' may also explain the saddle shape observed in upper site home range-scale resource utility functions, where selection probability increased slightly as 'distance to cover' and benthic velocity were both maximised (Fig. 3). While swift-moving water is generally described as a requirement for hellbenders (Bishop, 1941; Williams *et al.*, 1981), we emphasise that 'distance to cover' was consistently a stronger predictor of salamander selection than water velocity or meso-habitat. In effect, deep pools with dense arrays of boulders may represent higher quality habitat than shallow riffles where boulders are widely spaced, for captive-reared hellbenders.

Our findings have important implications for translocations of captive-reared Ozark hellbenders to the NFWR, and possibly for translocations involving other lotic species. The similarities between salamander selection patterns at the reach- and home range-scale indicates that abiotic attributes of candidate translocation sites should be considered at both scales. For example, we recommend that future translocation sites contain abundant cobble-boulder substratum within a reach, but the relative suitability of candidate sites should be determined based on average spacing between cobble and boulder and benthic water velocity within discrete patches of cobble-boulder substratum. The home range size of salamanders in our study averaged 33 and 10 m^2 at the upper and lower sites, respectively (C. Bodinof, unpubl. data). Therefore, we recommend considering abiotic attributes within habitat patches ≥10 m^2, and recommend selecting translocation sites where the combined extent of cobble-boulder patches equals or exceeds 10 m^2 per individual released. In patches where mean benthic water velocity exceeds 0.1 m s^{-1}, we recommend that spacing between coarse substratum average <1 m; and that spacing average <0.5 m when water velocity approaches 0.30 m s^{-1}. Our recommendations are based on data collected over 15 months and a range of seasons and discharge levels in the NFWR. However, the portion of the NFWR where our research was conducted is unimpeded by water control structures, and the contributing catchment is relatively intact (see study site description). As a result, the NFWR is subject to a relatively natural flow regime. Release sites within streams that are subject to flashy flow events, flows of extreme magnitude or spates of long duration should be considered carefully. We recommend evaluating the criteria presented here over a range of discharges rather than only during low summer or autumn flows when average water velocities are likely to be underestimated.

While our study indicates that the criteria we present will improve the odds that captive-reared Ozark hellbenders will settle in release sites, long-term monitoring is necessary to determine whether the translocated population persists. Because our goal was to investigate habitat attributes associated with short-term settlement and establishment of hellbenders, we restricted our study to examine associations between relatively fine scale resource characteristics and hellbender selection. We did not investigate how landscape-level factors may contribute to the persistence of the translocated population. Lotic systems can be described as hierarchical in organisation, where landscape-level characteristics govern the stream valley and upstream characteristics influence habitat downstream (Frissell *et al.*, 1983). Numerous studies have found that the factors influencing occurrence of a species at a broad scale (i.e. within a catchment or stream) differ from those influencing occurrence at a relatively fine scale (Johnson, 1980; Wiens, 1989; Rabeni & Sowa, 2002). Chemical pollution or siltation caused by landscape-level alterations within a catchment may reduce the likelihood that translocated populations will persist even if physical habitat meets the criteria we present here. Also, landscape scale attributes can determine the duration, intensity, magnitude and timing of high flow events (i.e. flow regime; Poff *et al.*, 1997). Therefore, relatively stable patches of microhabitat under a natural flow regime may no longer remain stable under an altered flow regime as a result of intensive land clearing, urbanisation, water diversion or impoundment. Other factors that we did not consider in our study and that likely play a considerable role in the settlement of translocated animals and long-term success of translocation include density and abundance of conspecifics, fine scale occurrence of prey or the presence of predators. We urge captive-rearing and translocation programs involving lotic species to consider whether landscape-level alterations within a catchment may doom translocation successes before investing resources in translocation efforts. We also encourage translocation programs to consider biotic factors as well as how the conditions of captive rearing, previous habitat or innate tendencies might influence selection for other species and in other streams.

Acknowledgments

We wish to acknowledge the University of Missouri, the Missouri Department of Conservation and the Saint Louis Zoo for logistic and financial support of this research. Handling associated with captive rearing and all surgical procedures were performed in entirety by the staff and interns of the Saint Louis Zoo according to institutional protocol. Monitoring of captive-reared animals took place under scientific collection permits issued by the Missouri Department of Conservation (# 13830 and 14180). We thank K. Goellner and the late R. Goellner for making this research possible. We thank T. Bonnot for help with data analysis, N. McClure for logistic support and R. J. Distefano, L. Goodrick, J. Howard, M. Sobotka, D. Jachowski, B. Ousterhout, S. Prutzman, J. Calfee, J. Ackerson, A. J. Pratt, and T. Crabill for assistance with field research. We are grateful to C. Rabeni, H. He, and two anonymous reviewers for comments on this manuscript.

References

Allan J.D. & Flecker A.S. (1993) Biodiversity conservation in running waters. *BioScience*, **43**, 32–43.

Anderson P., Turner M.G., Forester J.D., Zhu J., Boyce M.S., Beyer H. *et al.* (2005) Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *The Journal of Wildlife Management*, **69**, 298–310.

Armstrong D.P. & Seddon P.J. (2008) Directions in reintroduction biology. *TRENDS in Ecology and Evolution*, **23**, 20–26.

Baxter R.J., Flinders J.T., Whiting D.G. & Mitchell D.L. (2009) Factors affecting nest-site selection and nest success of translocated greater sage grouse. **6**, 479–487.

Benke A.C. (1990) A perspective on America's vanishing streams. *Journal of the North American Benthological Society*, **9**, 77–88.

Berger A.M. & Gresswell R.E. (2009) Factors influencing coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) seasonal survival rates: a spatially continuous approach within stream networks. *Canadian Journal of Fisheries and Aquatic Sciences*, **66**, 613–632.

Bishop S.C. (1941) Salamanders of New York. *New York State Museum Bulletin*, **324**, 1–365.

Bodinof C.M., Briggler J.T., Duncan M.C., Beringer J. & Millspaugh J.J. (2011) Historic occurrence of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* in hellbender *Cryptobranchus alleganiensis* populations from Missouri. *Diseases of Aquatic Organisms*, **96**, 1–7.

Bouckaert F.W. & Davis J. (1998) Microflow regimes and the distribution of macroinvertebrates around stream boulders. *Freshwater Biology*, **40**, 77–86.

Boyce M.S., Vernier P.R., Neilsen S.E. & Schmiegelow F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.

Briggler J.T., Utrup J., Davidson C., Humphries J., Groves J., Johnson T. *et al.* (2007) Hellbender population and habitat viability assessment: final report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN, U.S.A.

Briggler J.T., Larson K.A. & Irwin K.J. (2008) Presence of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) on hellbenders (*Cryptobranchus alleganiensis*) in the Ozark highlands. *Herpetological Review*, **39**, 443–444.

Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science, New York, NY, U.S.A.

Cooper A.B. & Millspaugh J.J. (1999) The application of discrete choice models to wildlife resource selection studies. *Ecology*, **80**, 566–575.

Cooper A.B. & Millspaugh J.J. (2001) Accounting for variation in resource availability and animal behavior in resource selection studies. In: *Radio Tracking and Animal Populations* (Eds J.J. Millspaugh & J.M. Marzluff), pp. 243–273. Academic Press, San Diego, CA, U.S.A.

Cope W.G. & Waller D.L. (1995) Evaluation of freshwater mussel relocation as a conservation and management strategy. *Regulated Rivers: Research & Management*, **11**, 147–155.

Federal Register (2010) Inclusion of the hellbender, including the eastern hellbender and the Ozark hellbender, in Appendix III of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In: *Federal Register* (ed. Weber W.), V.75, No. 173, pp. 54579–54585. U.S. Fish and Wildlife Service, Arlington.

Foster R.L., Mcmillan A.M. & Roblee K.J. (2009) Population status of hellbender salamanders (*Cryptobranchus alleganiensis*) in the Allegheny River drainage of New York state. *Journal of Herpetology*, **43**, 579–588.

Frissell C.A., Liss W.J., Warren C.E. & Hurley M.D. (1983) A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*, **10**, 199–214.

Gall B.G. & Mathis A. (2010) Innate predator recognition and the problem of introduced trout. *Ethology*, **116**, 47–58.

Gates J.E., Stouffer J., Ronald H., Stauffer J., Jay R. & Hocutt C.H. (1985) Dispersal patterns of translocated *Cryptobranchus alleganiensis* in a Maryland stream. *Journal of Herpetology*, **19**, 436–438.

Grobman A.B. (1943) Notes on salamanders with the description of a new species of *Cryptobranchus alleganiensis*. *Occasional Papers of the Museum of Zoology, University of Michigan*, **470**, 1–13.

Harig A.L. & Fausch K.D. (2002) Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications*, **12**, 535–551.

Heino J., Virkkala R. & Toivonen H. (2009) Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews of the Cambridge Philosophical Society*, **84**, 39–54.

Hillis R.E. & Bellis E.D. (1971) Some aspects of the ecology of the hellbender *Cryptobranchus alleganiensis alleganiensis*, in a Pennsylvania stream. *Journal of Herpetology*, **5**, 121–126.

Hoffman A.L., Olden J.D., Monroe J.B., Poff N.L., Wellnitz T. & Wiens J.A. (2006) Current velocity and habitat patchiness shape stream herbivore movement. *Oikos*, **115**, 358–368.

Howard J.K. & Cuffey K.M. (2003) Freshwater mussels in a California north coast range river: occurrence, distribution, and controls. *Journal of the North American Benthological Society*, **22**, 63–77.

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

Jachowski D.S., Millspaugh J.J., Biggins D.E., Livieri T.L., Matchett M.R. & Rittenhouse C.D. (2011) Resource selection by black-footed ferrets in South Dakota and Montana. *Natural Areas Journal*, **31**, 218–225.

Jaeger M.E., Zale A.V., Mcmahon T.E. & Schmitz B.J. (2005) Seasonal movements, habitat use, aggregation, exploitation, and entrainment of saugers in the Lower Yellowstone River: an empirical assessment of factors affecting population recovery. *North American Journal of Fisheries Management*, **25**, 1550–1568.

Jelks H.L., Walsh S.J., Burkhead N.M., Contreras-Balderas S., Diaz-Pardo E., Hendrickson D.A. *et al.* (2008) Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, **33**, 372–407.

Johnson D.H. (1980) The comparison of usage and availability measurements for evaluating resource preferences. *Ecology*, **61**, 65–71.

Joyce L. (2009) Movement patterns, home range and habitat selection by Kakapo (*Strigops habroptilus*, Gray 1845) following translocation to Pearl Island, southern New Zealand. University of Otago, New Zealand.

Kawamichi T. & Ueda H. (1998) Spawning at nests of extra-large males in the giant salamander *Andrias japonicus*. *Journal of Herpetology*, **32**, 133–136.

Malmqvist B. & Rundle S. (2002) Threats to the running water ecosystems of the world. *Environmental Conservation*, **29**, 134–153.

Mather M.E. & Stein R.A. (1993) Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading congener. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 1279–1288.

Mayasich J., Grandmaison D. & Phillips C. (2003) Eastern hellbender status assessment report. NRRI/TR-2003/09. U.S. Fish and Wildlife Service.

Michel P., Dickenson K.J.M., Barratt B.I.P. & Jamieson I.G. (2010) Habitat selection in reintroduced bird populations: a case study of Steward Island robins and South Island saddlebacks on Ulva Island. *New Zealand Journal of Ecology*, **34**, 237–246.

Murray S. & Innes J.L. (2009) Effects of environment on fish species distributions in the Mackenzie River drainage basin of northeastern British Columbia, Canada. *Ecology of Freshwater Fish*, **18**, 183–196.

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

Nickerson M.A. & Mays C.E. (1973a) *The Hellbenders: North American ''Giant Salamanders''*. Milwaukee Public Museum Press, Milwaukee, WI, U.S.A.

Nickerson M.A. & Mays C.E. (1973b) A study of the Ozark hellbender *Cryptobranchus alleganiensis bishopi*. *Ecology*, **54**, 1163–1165.

Oakleaf J.K., Murray D.L., Oakleaf J.R., Bangs E.E., Mack C.M., Smith D.W. *et al.* (2006) Habitat selection by recolonizing wolves in the northern Rocky Mountains of the United States. *The Journal of Wildlife Management*, **70**, 554–563.

Olden J.D., Kennard M.J., Lawler J.J. & Poff N.L. (2010) Challenges and opportunities in implementing managed relocation for conservation of freshwater species. *Conservation Biology*, **25**, 40–47.

Peterson C.L. (1988) Breeding activities of the hellbender in Missouri. *Herpetological Review*, **19**, 28–29.

Peterson C.L. & Wilkinson R.F. (1996) Home range size of the hellbender (*Cryptobranchus alleganiensis*) in Missouri. *Herpetological Review*, **27**, 2.

Peterson C.L., Reed J.W. & Wilkinson R.F. (1989) Seasonal food habits of *Cryptobranchus alleganiensis* (Caudata: Cryptobranchidae). *The Southwestern Naturalist*, **34**, 348–441.

Petokas P.J., Rogers J., Kratochvil P. & Sterngold N. (2006) Preliminary report on the distribution, habitat, and food preferences of juvenile and adult eastern hellbenders (*Cryptobranchus alleganiensis alleganiensis*) in northcentral Pennsylvania. *Journal of the Pennsylvania Academy of Science*, **79**, 120.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D. *et al.* (1997) The natural flow regime. *BioScience*, **47**, 769–784.

Porath M.T., Blasius H.B., Conn J.A., Young K.L. & Jacks L.S. (2010) Evaluating translocation of the Apache trout (*Oncorhynchus apache*) to nonhistorical renovated streams. *The Southwestern Naturalist*, **55**, 229–239.

Rabeni C.F. & Sowa S.P. (2002) A landscape approach to managing the biota of rivers and streams. In: *Integrating Landscape Ecology into Natural Resource Management* (Eds J. Liu & W.W. Taylor), pp. 114–142. Cambridge University Press, Cambridge, U.K.

Ricciardi A. & Rasmussen J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology*, **13**, 1220–1222.

Rittenhouse C.D., Millspaugh J.J., Hubbard M.W. & Sheriff S.L. (2007) Movements of translocated and resident three-toed box turtles. *Journal of Herpetology*, **41**, 115–121.

Rust P.J. (2010) Translocation of prespawn adult Kootenai River white sturgeon. *Journal of Applied Ichthyology*, **27**, 450–453.

Stamps J.A. & Swaisgood R.R. (2007) Someplace like home: experience, habitat selection and conservation biology. *Applied Animal Behaviour Science*, **102**, 392–409.

Statzner B. & Higler B. (1986) Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology*, **16**, 127–139.

Stuart S.N., Chanson J.S., Cox N.A., Young B.E., Rodrigues A.S.L., Fischman D.L. *et al.* (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Taber C.A., Wilkinson R.F. Jr & Topping M.S. (1975) Age and growth of hellbenders in the Niangua River, Missouri. *Copeia*, **4**, 633–639.

Taylor C.A., Warren M.L., Fitzpatrick J.R., Hobbs H.H., Jezerinac R.F., Pflieger W.L. *et al.* (1996) Conservation status of crayfishes of the United States and Canada. *Fisheries*, **21**, 25–38.

Townsend C.R., Dolédec S. & Scarsbrook M.R. (1997) Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biology*, **37**, 367–387.

Usio N. (2007) Endangered crayfish in northern Japan: distribution, abundance and microhabitat specificity in relation to stream and riparian environment. *Biological Conservation*, **134**, 517–526.

Wang X.-M., Zhang K.-J., Wang Z.-H., Ding Y.-Z., Wu W. & Huang S. (2004) The decline of the Chinese giant salamander *Andrias davidianus* and implications for its conservation. *Oryx*, **38**, 197–202.

Wentworth C.K. (1922) A scale of grade and class terms for clastic sediments. *Journal of Geology*, **30**, 377–392.

Wheeler B.A. (2007) *The Status, Distribution, and Habitat of Cryptobranchus alleganiensis bishopi* in Arkansas. PhD. Arkansas State University, Jonesboro, AR, U.S.A.

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

White G.C. & Garrott R.A. (1990) *Analysis of Wildlife Radio-Tracking Data*. Academic Press, San Diego, CA, U.S.A.

Wiens J.A. (1970) Effects of early experience on substrate pattern selection in *Rana aurora* tadpoles. *Copeia*, **3**, 543–548.

Wiens J.A. (1972) Anuran habitat selection: early experience on substrate selection in *Rana cascadae* tadpoles. *Animal Behaviour*, **20**, 218–220.

Wiens J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Williams D.R., Gates J.R., Hocutt C.H. & Taylor G.J. (1981) The hellbender: a nongame species in need of management. *Wildlife Society Bulletin*, **9**, 94–100.

Williams J.D., Warren M.L. Jr, Cummings K.S., Harris J.L. & Neves R.J. (1993) Conservation status of freshwater mussels of the United States and Canada. *Fisheries*, **18**, 6–22.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Rankings of hypothesised models representing reach-scale resource utility for captive-reared Ozark hellbenders (*Cryptobranchus alleganiensis bishopi*) released at two sites on the North Fork of the White River, MO, U.S.A., 2008–2009.

Table S2. Rankings of hypothesised models representing home range-scale resource utility for captive-reared Ozark hellbenders (*Cryptobranchus alleganiensis bishopi*) released at two sites on the North Fork of the White River, MO, U.S.A., 2008–2009.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organised for online delivery, but are not copyedited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

(Manuscript accepted 6 September 2011)