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Use of Restored Urban Habitat by Long-toed Salamanders (*Ambystoma macrodactylum*) in Seattle, Washington, USA

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Abstract.—**Habitat restoration in urban spaces can enhance amphibian migration, breeding, and foraging. The Amphibian Corridor is a habitat restoration project completed in 2015 that was designed to provide habitat for amphibians migrating between aquatic and forested areas in the Union Bay Natural Area (UBNA), Seattle, Washington, USA. To determine how amphibians use the corridor, we studied movement and microhabitat preference of Long-toed Salamanders (*Ambystoma macrodactylum*) in UBNA. We conducted weekly Visual Encounter Surveys for adults during the 2021 breeding season (December through April), and we also searched weekly for aquatic larvae and egg masses using dip bucket surveys. To identify individuals, we photographed and compared the dorsal spot pattern of each captured salamander. We used an online interface (capture-match.hoza.us) to enable citizen scientists to assist in matching photographs. During the study, we tallied 113 captures of 52 individuals, with some individuals captured 12 times. Fourteen of 19 recaptured salamanders were found in the same location as the initial capture, and the five salamanders that moved were found 12 m or less from their initial location. Within the corridor, Long-toed Salamanders preferred larger over smaller woody debris but showed no preference for the center of the corridor compared to the edges. Salamanders are using the Amphibian Corridor and other areas of UBNA; dorsal markings of adult Long-toed Salamanders are distinct; and individuals can be distinguished using a relatively inexpensive and non-invasive spot-pattern mapping method.**

Key Words.—conservation; habitat restoration; microhabitat; movement; spot-pattern mapping; urban ecology; woody debris

Introduction

Habitat loss is a major contributor to global amphibian decline (Collins and Storfer 2003). Restoration can counteract habitat loss for some species of amphibians by providing refugia, which may be particularly important in urban areas that otherwise are unsuitable (Holzer 2014). Restoration success depends on understanding amphibian responses to habitat: survival, colonization, and species composition in restored sites are influenced by various factors, including vegetation structure, pond depth, and the presence of invasive species (Purrenhage and Boone 2009; Shulse et al. 2012; Rowe and Garcia 2014 Hossack 2017; Díaz-García et al. 2020). Woody debris is a key habitat element because it provides sites where amphibians can shelter from predators, forage, and limit moisture loss (Mathis 1990; Whiles and Grubaugh 1996). Moisture retention increases with woody debris size, making coarse woody debris particularly important for some amphibians (Mathis 1990). For example, sites with coarse woody debris contain more species of frogs than sites without coarse woody debris (Evans et al. 2020). Banville and Bateman (2012) recommend adding woody debris to herpetofauna-focused rehabilitation sites in urban areas, though others acknowledge the need for research related to the use of these habitat features at small spatial scales (Scheffers and Paszkowski 2011).

Most amphibians migrate between forested habitat used during non-breeding seasons and aquatic habitat used for breeding activities, and habitat restoration efforts often seek to increase connectivity between these habitats (Rannap et al. 2009; Clauzel et al. 2015). Walter (2015) suggests that migration of amphibians, such as Long-toed Salamanders (*Ambystoma macrodactylum*), can be improved by increasing shade, leaf litter, cover objects, and soil moisture along potential migration routes. Understanding amphibian movement requires the ability to identify and track individuals, which can be logistically challenging, particularly if physical identification markers fall off or are expelled (Murray and Fuller 2000). Spot-pattern mapping provides a non-invasive means of distinguishing individuals of some species (Heyer et al. 1994), and it has been used with several species of salamanders, including Allegheny Mountain Dusky Salamanders (*Desmognathus*

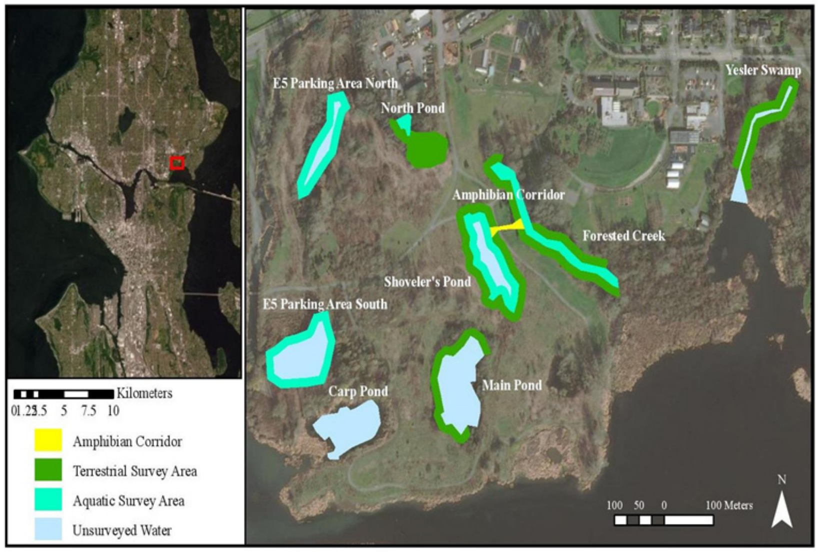

Figure 1. Areas surveyed for adult Long-toed Salamanders (*Ambystoma macrodactylum*) and egg masses in the Union Bay Natural Area in Seattle, Washington, USA. (Map created using ArcMap v10.7.1).

ochrophaeus; Forester 1977; Tilley 1980), Fire Salamanders (*Salamandra salamandra*; Speybroeck and Steenhoudt 2017), Jollyville Plateau Salamanders (*Eurycea tonkawae*; Bendik et al. 2013), Cave Salamanders (*Eurycea lucifuga*; Bradley and Eason 2018), Spotted Salamanders (*Ambystoma maculatum*; Grant and Nanjapa 2006), and Marbled Salamanders (*Ambystoma opacum*; Gamble et al. 2008). We explore the use of this technique with Long-toed Salamanders. To our knowledge, this technique has not been applied to this species, but the dorsal surface has variable yellow blotching patterns, which should be distinct enough to distinguish individuals.

We used spot-pattern mapping to distinguish individual Long-toed Salamanders and examined their use of woody debris as they moved within an urban habitat restoration site constructed to provide a pathway between terrestrial and aquatic habitats. Understanding the use of this site by amphibians can improve its adaptive management and facilitate the design of future restoration projects (Holl 2020). We hypothesized that where Long-toed Salamanders are found is affected by habitat characteristics. We predicted salamanders would be found more frequently under larger than smaller woody debris, and closer to the center, rather than the edges, of the corridor.

Materials and Methods

Study area.—We studied salamanders in the Amphibian Corridor, located in the Union Bay Natural Area (UBNA), Seattle, Washington, USA. UBNA is highly altered: it was first exposed when Lake Washington was lowered in the early 1900s and was a landfill from 1933 to 1964. The University of Washington has managed UBNA since 1971, primarily for restoration purposes (Ewing 2010). The Amphibian Corridor is about 50 m long by 5 m wide and was constructed in 2015 to connect a seasonal pond with a forested region (Fig. 1; Walter 2015). These habitats were previously separated by a grassy area and a gravel path, both of which are potential barriers for amphibian movement. For example, salamanders attempting to cross a gravel path lack cover that would allow them to avoid predators, desiccation, and bicyclists or pedestrians (Walter 2015). Construction of the corridor involved digging a ditch to increase soil moisture, adding plants and woody debris, and installing a culvert beneath the path. Although relatively little effort was made to survey amphibians inhabiting UBNA before installation of the Amphibian Corridor, Walter (2015) found an adult Long-toed Salamander at the Amphibian Corridor site and unidentified amphibian eggs in Shoveler's Pond.

Field surveys.—We conducted surveys in terrestrial and aquatic areas adjacent to and in the Amphibian Corridor (Fig. 1). We found Long-toed Salamanders during preliminary surveys (28 October to 31 December 2020; first salamanders found 30 November 2020). We did not search the entire survey area and did not record use of woody debris during preliminary surveys. During our focal period (4 January to 16 April 2021), we conducted one terrestrial survey and one aquatic survey each week. We alternated our surveys between daytime (starting between 0800 and 1100) and nighttime (starting 2 h after sunset), so that each week included either a daytime aquatic survey and nighttime terrestrial survey, or a daytime terrestrial survey and nighttime aquatic survey. We alternated survey locations and times to reduce the chances of missing a pulsed migration event and to capture adults during a wide range of activities (e.g., breeding, foraging, and resting).

As defined by Heyer et al. (1994), our terrestrial surveys were medium intensity Visual Encounter Surveys in which the lead author and a volunteer assistant searched the area within 10 m of the edge of the water by walking in zig-zags and searching under all cover objects (i.e., woody debris and human-made items, such as wooden boards or old signage). We also surveyed an area southeast of North Pond that contained an existing cover board array (Fig. 1). When we found a salamander, we recorded the date, time, GPS coordinates, and microhabitat features. We used the Avenza Maps app (Avenza Systems Inc., Toronto, Ontario, Canada) on a Google Pixel 3a smartphone (Google Inc., Mountain View, California, USA) and maps made in ArcMap version 10.7.1 to track observations spatially. We placed salamanders in a plastic tub and photographed their dorsa on a high-contrast background using a Google Pixel 3a smartphone camera (resolution = 4032 × 3024 pixels). Our hands were gloved or wet during handling to minimize stress to the salamanders. We assigned each capture, individual, and photograph a unique number. Between salamander captures, we sanitized the tub using an isopropyl alcohol spray to prevent disease spread.

Logs from a trunk and branches of a tree used as cover objects were installed in the Amphibian Corridor between 2015–2019. Square plywood boards (0.3–1.2 m) were used as cover objects near North Pond, but we do not know when they were installed. In other areas, cover objects included natural logs and trash (e.g., cardboard and metal signs). We mapped the locations of all cover objects and measured their size as maximum log diameter or board length using ArcMap version 10.7.1 (Esri, Redlands, California, USA). For woody debris in the Amphibian Corridor, we also measured the distance from the center of the ditch to the closest edge of each object.

During daytime aquatic surveys, we searched primarily for egg masses and larvae to determine where breeding was occurring. To help find egg masses and larvae, we dipped a bucket in the water approximately every 5 m (far enough apart to be considered independent; Heyer et al. 1994). We recorded GPS coordinates and a brief description of the substrate when we observed eggs or larvae. Other than using a bucket to search for egg masses and adults, we followed the Amphibian Monitoring Protocol of the Woodland Park Zoo when conducting surveys (www.zoo.org/amphibianmonitoring). According to this protocol, surveyors walked the perimeter of the pond in the shallow water (< 1 m depth) searching visually for egg masses. We recorded survey time and GPS coordinates for any egg masses or amphibians found.

During nighttime aquatic surveys, we searched primarily for breeding adults, which we captured with a bucket. We searched from shore where possible to avoid disturbing egg masses. When we found adults, we recorded GPS coordinates and photographed them as described for the terrestrial surveys.

Spot-pattern mapping.—After each survey, the lead author compared the spot patterns of the newly photographed individuals to those captured previously, and assigned each unique individual an identification number. We used a citizen science approach to confirm these assignments. A volunteer developed a website, Capture-match (http://capture-match.hoza.us), that displayed two photographs at a time. Volunteers compared the spot patterns on the two images, decided whether they represented the same or different individuals and clicked the appropriate button (Fig. 2). Volunteers clicked Same if they believed the same individual was shown in both images, and Different if they believed

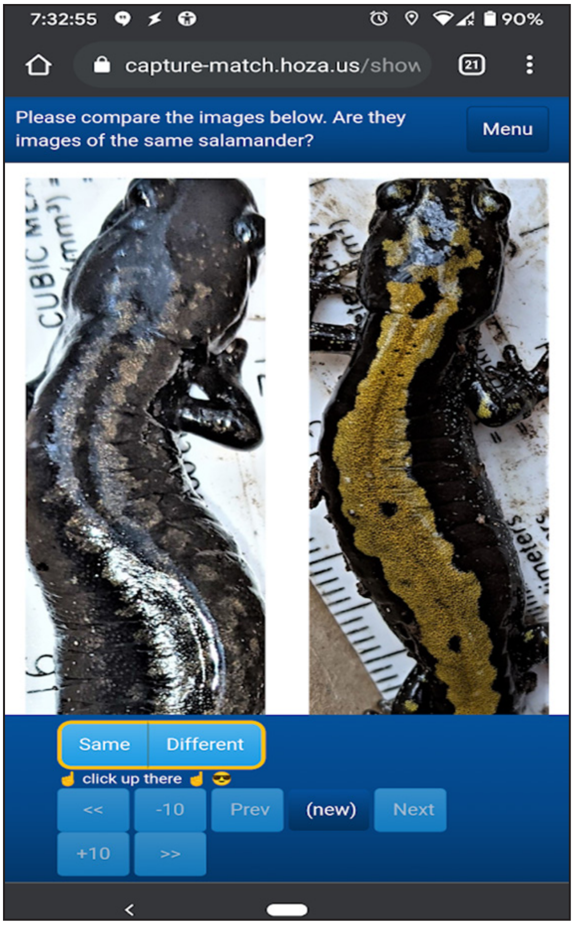

Figure 2. Screenshot of the website (capture-match.hoza.us) allowing volunteers to match individual animals from different capture events. The screenshot shows the view from a mobile phone, but the website could also be accessed via a laptop or personal computer. The website displayed all possible pairs of images from different surveys.

the images showed different individuals, and their responses were automatically recorded on a spreadsheet. The website could be accessed on either a computer or a mobile device. We assumed no salamanders were recaptured during a survey event and, therefore, we only paired photographs from different surveys. We excluded preliminary surveys from this analysis because those images were not organized by survey date. During the focal survey period, we constructed 3,567 photograph pairings, and each pair was reviewed by at least three volunteers to determine if the pairing was of the same or different individuals. We processed volunteer responses in Excel and R (R Development Team 2018) using the packages Tidyverse (Wickham 2021) and Writexl (Ooms 2021). We considered an image pair to show the same individual if indicated as same by at least two-thirds of the volunteers who evaluated it. The source code and website development methods are available from https://github.com/bowtie-ltsa/manual-image-match under the GNU General Public License.

Movement analysis.—We combined spot-pattern mapping results with geographic coordinates to determine movements of individual salamanders. We viewed movement locations in ArcMap version 10.7.1 (ESRI 2019), and we created a map of all observation locations. We visualized the timing of salamander captures across the study period using the R package ggplot2 (Wickham et al. 2021). To determine whether more salamanders were captured during the day or night, we used the glm() function in R Studio with a Poisson distribution (R Development Core Team 2018). We used egg mass locations to understand habitat patches being used by salamanders.

Microhabitat preference.—Our analyses of microhabitat preference focused on woody debris in the Amphibian Corridor, and on salamander observations from 14 January to 16 April 2021 (earlier surveys did not track under which woody debris each individual was found). We combined the size and distance from the center of the corridor with a binary indicator of whether a salamander was detected beneath woody debris at any point during the study period (Supplemental Information Table S1). We analyzed 39 pieces of woody debris ranging from 12–54 cm in diameter and 0–310 cm from the center of the Amphibian Corridor. We used Generalized Linear Models (GLM; glm() function; R Development Core Team 2018) to determine whether salamander presence varied with woody debris size and distance from center of the corridor, testing variables separately and in interaction with one another (see Supplemental Information pp. 5–12 for code). All GLMs used the binomial family and logit link function because presence is a binary response. We used AICc scores (R package MuMIn; Bartoń 2020) to identify a parsimonious model, and we considered variables significant at $P \leq 0.05$. We visualized models by their estimates and 95% confidence intervals.

Results

We found Long-toed Salamanders around five of the seven aquatic areas surveyed at UBNA (Fig. 3). Six years after construction, salamanders were present within the Amphibian Corridor and were using aquatic habitats on both sides of the site in the surrounding park to lay eggs. We found 13 of the 19 egg masses in North Pond, which is not adjacent to the Amphibian Corridor (Fig. 3). We documented no movements between ponds, and 14 of 19 recaptured salamanders were under the same piece of woody debris at initial and subsequent captures. Furthermore, salamanders were more likely to be found under larger woody debris compared to smaller ($Z = 2.142$, $P = 0.032$; Fig. 4).

Spot-pattern mapping.—We tallied 88 captures during the focal period (January-April). The assessment of the lead author and the independent volunteers were consistent: both indicated that these captures represented 40 individuals. We, therefore, assumed that assessments by the lead author during the preliminary surveys were also accurate. Across the entire study period, we tallied 113 captures of 52 individuals. We recaptured individuals up to 4.5 mo after the initial capture and observed no differences in color pattern, even in very small markings (Fig. 5). Of particular note was one individual that was molting during recapture; its spot pattern after molting was identical to that in

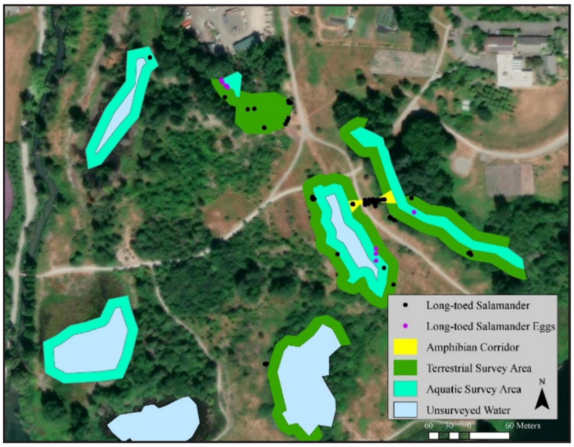

Figure 3. Locations in the Union Bay Natural Area in Seattle, Washington, USA, at which Long-toed Salamanders (*Ambystoma macrodactylum*) were captured (black dots; n = 113) and Long-toed Salamander egg masses were found (purple dots; n = 19). Surveys were conducted from December 2020 to April 2021, with one terrestrial survey and one aquatic survey each week. (Map created using ArcMap v10.7.1).

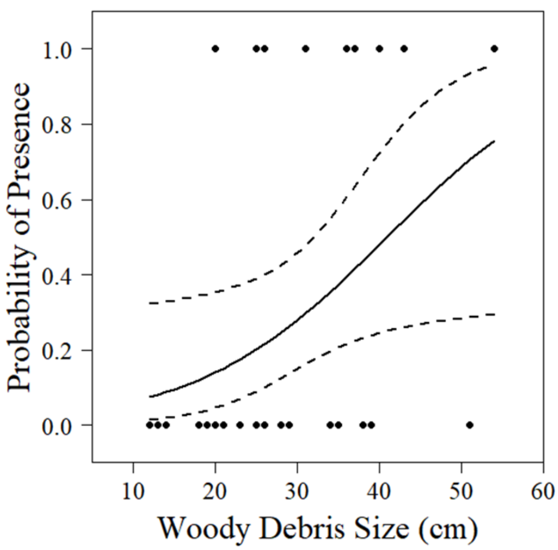

FIGURE 4. Generalized Linear Model showing the probability of at least one Long-toed Salamander (*Ambystoma macrodactylum*) being found under a piece of woody debris as a function of woody debris diameter. The solid line is the predicted probability of presence at a given woody debris size, and the dashed lines are the 95% confidence interval for the prediction. Black dots show the observed data, with each dot representing a piece of woody debris (n = 39) surveyed weekly during the focal period.

a photograph taken two weeks earlier under the same piece of woody debris (Fig. 5).

Movement.—We captured 1–12 salamanders per survey. Movements did not appear to be episodic because there were no obvious pulses in salamander occurrence (Fig. 6). We captured 25 individuals within the Amphibian Corridor; the other individuals were scattered among other locations at UBNA (Fig. 3). Time of survey (day vs. night) did not significantly impact the number of individuals found ($Z = 1.413$, $P = 0.158$; Fig. 6). Most salamanders were found under logs or cover boards during terrestrial surveys; only one was found swimming during an aquatic survey.

We used egg mass locations to approximate the aquatic areas that salamanders used and might move within or between. From 18 February to 15 April 2021, we found egg masses on both sides of the Amphibian Corridor: three eggs were laid singly in Shoveler's Pond and three egg masses (with a total of about eight eggs combined) were in the Forested Creek. In the other part of the survey area, 13 egg masses were in North Pond (with 2–23 eggs per mass; Fig. 3).

Based on spot-pattern mapping, 61 of the 113 captures were recaptured individuals, which represented 19 of the 52 individuals identified. Only five individuals were captured in two or more locations. The greatest distance measured between initial and final captures was 12 m, but most individuals were found under the same piece of woody debris.

Microhabitat preference.—Within the Amphibian Corridor, salamander presence was positively related to size of woody debris ($Z = 2.142$, $P = 0.032$; Fig. 4) but was not related to distance to the center of the Amphibian Corridor ($Z = -1.389$, $P = 0.165$). The interaction between woody debris size and distance to center was also not significant ($Z = -0.679$, $P = 0.497$). Long-toed Salamanders preferred larger woody debris at least up to about 50 cm in diameter over smaller woody debris, and there was only a 25% chance of finding a salamander

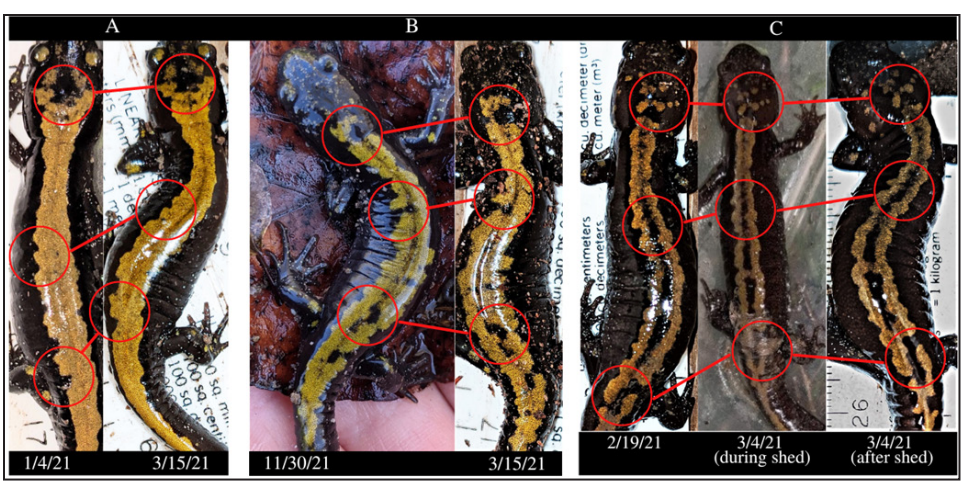

FIGURE 5. Examples of the distinctive spot patterns used to distinguish three individual salamanders (panels A, B, and C, respectively) on different dates. The connected red circles highlight the same patterns in successive photographs. Note that some dirt was present in both 15 March 2021 photographs but not in earlier photographs. The images in (C) show a Long-toed Salamander before, during, and after molting. Note the dead skin on the tail in the middle and right-hand photos and the similarity of the spot patterns before and after molting. Photographs edited to enhance sharpness and contrast. (Photographed by Julianna C. Hoza).

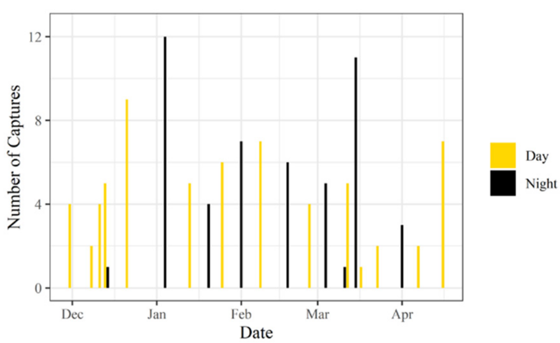

Figure 6. Number of Long-toed Salamanders (*Ambystoma macrodactylum*) captured during surveys in the Union Bay Natural Area, Seattle, Washington, USA, from December 2020 to April 2021. No extreme peaks in observations were obvious given the sample size, and there was no statistical difference between the number of captures at night (black) compared to during the day (gold). All surveys shown are terrestrial except 17 March 2021, when we encountered a salamander on land during an aquatic survey. Preliminary surveys, conducted between 30 November and 14 December 2020, surveyed less area than the standard. The survey on 16 April 2021 had higher survey effort and a slightly different, but similarly sized, area.

under a piece of woody debris 28 cm or less in diameter at any point during the study.

Discussion

The use of the Amphibian Corridor by Long-toed Salamanders indicates the potential for successful habitat restoration, at least according to Walter (2015), who expected salamanders to use woody debris within the site. Walter (2015) also predicted that amphibians, including Red-legged Frogs (*Rana aurora*) and Pacific Chorus Frogs (*Pseudacris regilla*), would use the corridor for migration; however, we observed no frogs using the site and could not verify migration through the corridor. Our data also demonstrate that Long-toed Salamanders show high site fidelity, often using the same woody debris for weeks at a time. This behavior has not been described previously for Long-toed Salamanders and is information that can be useful for land managers involved in restoration planning.

Spot-pattern mapping.—Spot-pattern mapping is an effective method to identify individuals in a variety of taxa (Haxton 2021; Osterrieder et al. 2015; Caci et al. 2013), and it has advantages over other methods of marking individuals. For example, toe-clipping can be ineffective (Heyer et al. 1994), radio or passive integrated transponder (PIT) tags can be expensive, and dye injections and toe-clipping can negatively impact amphibians (Heyer et al. 1994; Murray and Fuller 2000). Besides avoiding these issues, spot-pattern mapping can be performed by many people, either by eye or with use of software programs. For example, volunteers had a 96% chance of correctly matching individual salamanders using by-eye identification (Grant and Nanjapa 2006). Other studies have used Wild-ID software (Bolger et al. 2012) to identify individual amphibians (Bendik et al. 2013; Mettouris et al. 2016; Aevarsson et al. 2022), though our preliminary testing of the software was unsuccessful (see Supplemental Information). Caci et al. (2013) and Sannolo et al. (2016) also identified individual organisms using I^3S (Interactive Individual Identification Software; Van Tienhoven et al. 2007). The simple internet platform developed by one of our volunteers allowed many volunteers to contribute to the matching process, and our data indicate that this technique is an effective and inexpensive method for identifying individual Long-toed Salamanders.

A key assumption of spot-pattern mapping is that patterns remain constant throughout the development and growth of individuals of the focal species, at least for the duration of a study. Consistency of dorsal markings is apparently variable among species of salamanders. For example, patterns are stable for at least 7 y in adults of some species (Tilley 1980), but dramatic changes in spot pattern occur within a year in others (e.g., Eastern Tiger Salamanders, *Ambystoma tigrinum*; Waye 2013). We did not permanently mark salamanders when they were first caught, so it is possible some identification by markings could be incorrect, but because of the complexity of Long-toed Salamander spot patterns, we doubt different individuals have identical patterns. Furthermore, the probability is low that individuals with indistinguishable patterns will inhabit the microhabitat underneath the same piece of woody debris. Finally, our data indicates that patterns are not affected by molting, which occurs from 4–20 d of capture in some species of ambystomatid salamanders (Licht and Bogart 1987). Although we doubt that patterns change substantially during the season-long timeframe of this study, additional information is necessary to confirm the consistency of spot patterns for longer periods of time. We suggest that salamanders reared in captivity or those tracked with PIT tags or radio telemetry could be photographed periodically to better evaluate the usefulness of spot-pattern mapping for long-term studies involving Long-toed Salamanders.

Movement.—Long-toed Salamanders use the Amphibian Corridor throughout the breeding season. We do not know how quickly or how far individuals move, but some were recaptured up to 12 m from the original collection locations. Based on egg masses, Long-toed Salamanders breed in water bodies on both sides of the Amphibian Corridor (e.g., Shoveler's Pond and the Forested Creek), but no salamanders were captured in breeding ponds and at terrestrial sites; consequently, we do not know if salamanders travel through the Amphibian Corridor to get to these breeding sites.

Woody debris within the Amphibian Corridor can serve as a refuge for Long-toed Salamanders during periods of stress. For example, an injured salamander missing a foot and with no mobility in the leg remained underneath a log for at least 11 weeks. During the time spent beneath the log, the foot was regenerating and at least one toe was fully regrown after 11 weeks. Although metabolic processes may be different for injured salamanders, this individual also provides evidence for spot pattern stability, because it could be identified both by its missing foot and by its dorsal pattern.

Long-toed Salamanders migrate seasonally (Beneski et al. 1986), but most recaptures were of salamanders that remained in their original capture location, suggesting that they have small home ranges during the breeding season. We do not know the fate of individuals that were not recaptured; for example, whether they moved longer distances, burrowed underground, or died. Also, salamanders inhabit UBNA at least from late November through mid-April (30 November 2020 and 16 April 2021, when surveys ceased), indicating that salamanders either remain in the study site for several months, or are residents and only migrate short distances to breed. Other ambystomatid salamanders migrate 100–300 m (Semlitsch 1981), but salamanders in UBNA may have moved even shorter distances because adults remained within 50 m or less of pond edges throughout the study.

Long-toed Salamanders are the only species of amphibian known to use the Amphibian Corridor, but American Bullfrogs (*Lithobates catesbeianus*) occur in other parts of UBNA (Supplemental Information file). Because they are invasive and predatory (Corkran and Thoms 2006), American Bullfrogs potentially affect salamander breeding success and distribution within UBNA. Additional research is required to better understand interactions between native and invasive amphibians in restored urban sites.

Microhabitat preference.—The lack of correlation between Long-toed Salamander presence and distance to the center of the Amphibian Corridor was unexpected because the corridor was designed to provide more shade, leaf litter, and soil moisture than is available in the surrounding grassland. One possibility for the lack of correlation is that there is no gradient of soil moisture or shade from the edges to center of the corridor; salamanders also may show no preference for the Amphibian Corridor over the unrestored grassy area to the sides of the restoration. Future studies should compare soil temperature and moisture across the gradient from center to edges of the site.

Long-toed Salamanders prefer larger woody debris over smaller woody debris, which is consistent with other studies that indicate that large woody debris provides higher quality habitat for amphibians than smaller woody debris (Ober and Minogue 2007; Todd 2009). The narrow range of sizes of woody debris present on site limits our ability to determine best size of woody debris. We suggest installing a wider range of diameters of woody debris than used at UBNA and then comparing the relative use of the different sized debris by salamanders to better determine the most effective size of debris to be used when restoring amphibian habitat. Nonetheless, we recommend that habitat restoration for Long-toed Salamanders include woody debris with > 40 cm diameter as our model predicts that such pieces have a > 50% chance of being used by salamanders during the breeding season. Similar studies could be conducted in other systems to determine threshold woody debris sizes for other species and in other locations because woody debris use may vary depending on canopy cover (Strojny and Hunter 2009) or prey availability (Gabor 1995). Future research could also consider woody debris density or spacing, wood type, depth under soil surface, or substrate beneath debris, to determine the key elements to incorporate into habitat restoration prescriptions for species of conservation concern.

Limitations.—Little information is available on demography or abundance of amphibians at UBNA before construction of the Amphibian Corridor. Walter (2015) indicates species she encountered, but does not report abundances; consequently, comparisons of use of the Amphibian Corridor before and after restoration is not possible. Furthermore, the scarcity of woody debris outside of the corridor makes determination of salamander occurrence difficult. Comparing use within and outside of the corridor requires either a cover board experiment, or using telemetry to track individuals over time, which was beyond the scope of this study. The use of cover boards would alter the restored habitat; because of this, we chose to only assess the use of the corridor by salamanders without comparing the corridor and surrounding regions or the area before and after restoration.

Conclusions.—Long-toed Salamanders occur in several areas within the Union Bay Natural Area, including the Amphibian Corridor. Spot-pattern mapping allows us to distinguish individual Long-toed Salamanders and can be used in other citizen science projects. Furthermore, we show that, six years after construction of the Amphibian Corridor, during their breeding period Long-toed Salamanders preferentially use larger woody debris, show high site fidelity, and use wetlands on both sides of the corridor as oviposition sites.

Acknowledgments.—We thank Bradley Hoza for creating capture-match.hoza.us, the website that volunteers used to compare individual salamanders. We also thank Laura Prugh, who allowed work under Institutional Animal Care and Use Committee protocol #4381-02 and Washington State Scientific Collections Permit #21-066 to conduct aquatic surveys and terrestrial surveys, and we thank Katie Remine at the Woodland Park Zoo, who allowed us to use her citizen science protocol to survey egg masses. We thank the volunteers who helped with field work: Leila Arafeh, Ash Baldino, Christie Caldwell, Alex Coenen, Georgia Coleman, Sarah Crumrine, Erik Ertsgaard, Jackson Hall, Jessica Matyas, Zara Ramerman, and Nikoli Stevens. We also thank those volunteers who helped match individual salamanders using capture-match.hoza.us: Emily Anderson, Leila Arafeh, Marijka Bakker, Sophia Boyd, Holly Brock, Charlotte Gerzanics, Ava Jeane Gutheil, Jackson Hall, Larry Hall, Maya Hall, Rebecca Johnson, Alyson Liu, Ruby O'Malley, Zara Ramerman, Andy Samms, Tam Ta, Alicia Torres Hoza, Daniel Tran, Martha Work, and Diane Yeh. Lastly, we thank Timothy Jones for assistance with statistical analysis.

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